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III

CONTENTS OF VOLUME V.

No. 1.—The Dakota-Permian Contact in Northern Kansas... *F. C. Greene.*

2.—Further Notes on the Pueblo Ruins of Scott County, *H. T. Martin.*

3.—The Influence of Magnesium Sulphate on the Motor Cells of the Cerebral Cortex.... *H. F. Hyndman and W. E. Mitchner.*

4.—A Study of the Respiratory and Cardiac Activities of the Skate following Intravenous Injection of Salt Solution... *Ida Hyde.*

5.—Nutrition of the Embryo Sac and Embryo in Certain Labiatæ, *F. H. Billings.*

6.—Mitosis in the Root Tips of Podophyllum peltatum, *Aute Richards.*

7.—Koeberlinia spinosa Zucc. : An Ecological Study of the Anatomy of the Stem and some other parts.. *Miriam Sheldon.*

8.—A Case of Absolute Tone Memory................ *Archibald Hogg.*

9.—The Hackberry Psylla, Pachypsylla celtidis-mammæ Riley: A Study in Comparative Insect Morphology ..... *H. B. Stowe.*

10.—Investigations Regarding the Phloëm and Food Conduction in Plants.............................. *Frank U. G. Agrelius.*

11.—Histology of Townsendia exscapa and Lesquerella spathulata, *Lillian Bunton.*

12.—Cell Changes in the Alveoli of a Carcinoma of the Mamma, *Earl F. Clark.*

13.—The Temnospondylous Amphibia and a New Species of Eryops from the Permian of Oklahoma................ *Roy L. Moodie.*

14.—An Armored Dinosaur from the Cretaceous of Wyoming..... *Roy L. Moodie.*

15.—A Contribution to the Soft Anatomy of Cretaceous Fishes, and a New Promitive Herring-like fish from the Texas Cretaceous.................................... *Roy L. Moodie.*

16.—A New Species of Holotrich........................ *Nadine Nowlin.*

17.—Orthoptera from the Santa Rita Mountains, Arizona, collected by the University of Kansas Expedition...... *Jas. A. G. Rehn.*

18.—Observations on the Gryllidæ: III. Notes of the Classification and Some Habits of Certain Crickets, *W. J. Baumgartner.*

19.—Observations on the Gryllidæ: IV. Copulation, *W. J. Baumgartner.*

20.—An Examination of the Chromosomes of Anasa tristis....... *C. E. McClung and Edith Pinney.*

21.—Foundations of Arithmetic................. *Arthur Bolles Frisell.*

207.

THE
KANSAS UNIVERSITY SCIENCE BULLETIN.

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CONTENTS:

Cell Changes in the Alveoli of a Carcinoma of the Mamma, *Earl F. Clark.*

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3310

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CELL CHANGES IN THE ALVEOLI OF A CARCINOMA OF THE MAMMA.

BY EARL F. CLARK.

(Contribution from the Zoölogical Laboratory, No. 188.)

Submitted in partial fulfillment of the requirements for the degree of Master of Arts.

Plates XLVI to XLVIII.

THE literature upon the pathological new growths of the human body scarcely mentions amitosis as a method of cell increase. It occurred to me to treat in a comparative way the two methods of cell division, mitosis and amitosis, as they are found in neoplastic material.

It is not intended to make this paper conclusive, but to make it the first of a series of case studies from the results of which a general conclusion may be deduced as to the relative importance of indirect and direct cell division in these new growths.

I am indebted to Dr. M. T. Sudler for the following history: "In the first week of October, 1907, she fell, bumping the breast against a hard object. No further notice was taken of the incident, however, until the latter part of November, when she noticed a hard, thin, round lump in the right breast about the size of a silver dollar. It was then freely movable. About the 25th of December she noticed a tingling in the right arm, and on January 1, 1908, the arm began to ache. The original mass increased rapidly in size until the whole breast was involved. Its rate of growth seemed intermittent, some weeks being much more rapid than others. Upon examination the entire breast was found to be occupied by a hard, firm mass, which was intimately incorporated in the connective tissue of the breast. The nipple was somewhat retracted but not completely. The mass was movable over the muscle. The axillary nodes were enlarged and hard. On February 5 the breast, together with the axillary lymph nodes, was removed. On March 13 a recurrence in the left breast was discovered, which was removed on March 20. Twelve days later metastatic nodules in the neck were removed. The patient died soon afterwards from an apparently general carcinomatous involvement of the body. From the foregoing history it is plain that this was an extreme type of the most rapidly growing and malignant of tumors."

This material was not prepared especially for fine cytological work because the discovery of its excellence for investigation was not made until after its fixation. It was fixed in ten-percent formalin and remained in a weaker solution until used. I found the cell nests somewhat shrunken away from the surrounding stroma and the chromatin either so swollen or so poorly preserved that I was unable to make out details in regard to the chromosomes. The fixation otherwise was good. The tissue was mounted in paraffin and cut in sections eight micra thick. Sections were stained in hæmatoxylin for twelve hours after being in a mordant of iron-alum for twelve hours. They were then decolorized in the iron-alum solution to the desired extent.

The cells studied appeared in variously shaped pockets or alveoli surrounded by dense white fibrous connective tissue. This connective tissue stroma was penetrated more or less by columns of tumor cells, one to three cells in diameter. In short, this specimen in parts conformed to the scirrhus while in others it was more of the medullary type of carcinoma. In this paper I will confine my study to the cell nests or alveoli.

In the first four figures I chose a typical field from widely separated parts of the tumor for each drawing, and drew all the structures appearing in that field. I did this to show the similarity of the cell content of the tumor mass throughout. The normal resting cell, with its variation in size, shape and chromatin content, composed the greater number of cells of each group. It was considered the normal resting cell because of its uniform staining quality, its maintenance of cell and nuclear wall, its content of regularly outlined chromatin nucleoli within a single nucleus. Marked variation in any of these characteristics was considered a cell change having as its ultimate end either the production of new cells or degeneration.

Among the resting cells were others which could be easily identified as being in the process of indirect division. Although no detail of the chromosomes could be made out, yet the increased amount of chromatin over the resting cell, its affinity for the stain, the irregular outline of the chromosomes, the absence of the nuclear membrane and the shape and position of the chromatin masses identical with those of the prophase, metaphase, anaphase, and telophase leave no doubt as to the identity of such cells. Equally distributed among the resting cells were other cells which were clearly abnormal, owing to their unusual size and their content of two or more nuclei or clefts of greater or less depth which either separated or tended to separate the single nucleus into two or more distinct segments. These separated segments had all the characteristics of the nucleus of the resting cell. I have considered such cells as in the process of direct cell division, although I have been unable to find a single cell showing distinct separation of the cytoplasm. Adami thus describes amitosis: "The nucleus divides without any apparent preliminary rearrangement of its structure. It becomes elongated, then dumb-bell shape (the process can be followed in the amœba), the connecting neck becomes broken across and the two daughter nuclei pass apart, their separation being in some cases followed by division of the cell body while in others this further division is wanting and the binucleate cell is produced." Patterson, in "Amitosis in the Pigeon's Egg," says: "In most cases the nucleus elongates in the direction transverse to the plane of the future division, after which a constriction in the nuclear membrane appears about the entire circumference of the nucleus. This constriction continues to deepen until a complete division is effected. A modified form of this type is found in those cases in which the constriction proceeds from one side."

Although the process in this material differs somewhat, I think, from that described by Adami and Patterson for other material, the result is the same. Therefore I feel safe in assuming that cells with the nucleus wholly or in various degrees of separation are in the process of amitosis. Ziegler and Vom Rath consider such cells as already in the process of degeneration. If so, it will not be out of place to consider along with these division figures structures that appear throughout this material and which are plainly cells in varying degrees of degeneration, as evidenced by changes in the chromatin, cytoplasm and cell wall, and note if there is any similarity between them.

Figures 5, 6, 7 and 8 are used to further illustrate these three cell changes as they appear in various parts of the tumor. In these drawings I omitted the greater number of the resting cells.

I will supplement this preliminary account by short descriptions of individual cells in the several plates with interpretations of their variation from the normal.

I have used the term "cell nests" to mean the group of cells within the alveoli; the term "chromatic cells" to mean those cells in that condition in the degeneration process just before the chromatin loses its staining power and when it has swollen so much and become so diffuse as to fill the entire nucleus as a more or less densely staining mass.

OBSERVATIONS.

The Cells of the Nests Change by Mitosis, Amitosis and Degeneration.

In showing the cell changes of these nests I will simply use a number of figures, describing each one with some amount of detail and inserting comments as observations suggest.

FIGURE 1 is drawn from cell nest 2. It includes three cells dividing directly, one dividing indirectly, two cells in the process of degeneration, and a number of resting cells.

The resting cell is smaller than the dividing cell, is of polyhedral shape, has a limiting membrane, and a large, well-marked nucleus. Its cytoplasm is denser than the karyoplasm and is of a reticular appearance. The nucleus has a well-marked nuclear wall and usually contains from one to three regularly round, deeply-stained chromatic bodies which I will call chromatin nucleoli. A directly dividing cell is of much larger size than the resting cell and usually a bit clearer, a condition suggesting that it has included a large amount of fluid preparatory to its division. The nucleus divides by the formation of a groove or cleft on one side. I have not seen a cell where the cleft appeared on the two sides. The cleft deepens and the nuclear substance pulls apart to form the regular outline of the daughter nuclei. The nuclear membrane seems to follow the deepening cleft so that as soon as the segments have separated the karyoplasm is enclosed by its wall.

In the cells shown I have drawn them as they appeared in outline in one plane, but included the chromatin through the depth of the cell. Each well-defined segment of the nucleus usually contains a chromatin nucleolus. In cell *A* the lower nuclear segment has a second cleft appearing upon its inner border. Cell *B* has two distinct nuclear segments, each one of which has a secondary groove appearing upon its upper surface. The upper segment shows no chromatin at all. Cell *C* shows two nuclear segments, each containing a chromatin nucleolus. Cell *D* shows a central constriction of its nucleus with the mother chromatic mass in the plane of constriction, but I do not say it is in the process of division.

Cell *E* is a representation of the typical indirect division figures found in this material. It is in the early anaphase. As I have already said, this material, being fixed in formalin with no particular care regarding its cytological preservation, shows no detail characteristics of the chromosomes. I have used in my counts only the well-marked division figures, from the close spireme stage on. In these indirect divisions the cells are larger than the resting cells, the nuclear membrane had disappeared, and about the chromatic figure the cytoplasm was clear. I was unable to make out the spindle or any of the details farther than shown.

Cells *F F* are two fragments of degenerated cells in each of which the chromatin has swollen and coalesced into one homogeneous, deeply staining mass.

FIGURE 2. Among the cells of this group there is not the noticeable difference in size usually seen between the dividing cells and the resting ones. Cell *A* shows an indirect division plainly. Cell *B* shows the nucleus being divided by a cleft passing in from its upper surface. Each segment contains a chromatin nucleolus. Cell *C*, an otherwise ordinary resting cell, contains in its cytoplasm, half way from the cell border to the nuclear membrane, a clear vesicle, regular in outline and with a definite limiting border indicating that it is filled with a substance differing from the cytoplasm.

FIGURE 3 shows no new structures, but attention is called to the regularity of the chromatin nucleoli. Cells *A* and *B* show the nuclei entirely segmented and each segment containing regular chromatin nucleoli, the lower segment of cell *B* containing two.

FIGURE 4 is a group of twelve tumor cells drawn from cell nest 1, a small nest of seventy-five cells containing six indirect and no direct divisions. In this group are shown four of the six indirect divisions. Cells *A* and *B* are noticeable for their large size, while cells *C* and *D* are of the same size as the resting cells. Cell *E* is a common-sized resting cell, containing one chromatin nucleolus but with a hollow clear vesicle bulging into the wall of its nucleus. Cell *F* is a common resting cell except that it has its chromatin diffused through the karyoplasm.

FIGURE 5. In this group and in those following I have not included all the cells that appeared in the field, but simply instructive ones and enough resting cells to show a comparison. The group was drawn from cell nest 3, of 253 cells, which included six indirect and five direct divisions. Cell *C* was in the fourth tier from the edge and on the peripheral side of the group. It was large, being .0125 mm. in its greatest diameter and showing a nucleus in two segments, each segment containing a regularly round chromatin nucleolus. The cell was noticeably clearer than the others. Cell *B* also has a bisegmented nucleus, but its chromatin was scattered in irregular masses through the karyoplasm. It was also large, being .01 mm. in its greatest diameter. The nucleus of cell *A* was in three segments, each part having a regularly round chromatin nucleolus, and beside this a certain amount of chromatin scattered in clumps through the karyoplasm. It was .0125 mm. in its greatest diameter. In all my cell measurements I used a micrometer scale which I have found by measurement to give the following dimensions: With a drawing board on a level with the object and at the same inclination as the microscope stage, using 1/12 oil-immersion objective and a 8× Huyghenian ocular, an object that fills the square of the scale is .0125 mm. in diameter; with the 1/6 objective it is .03 mm. in diameter, and with a 2/3 objective it is .15 mm. in diameter. Three-fourths of the square equals .0093 mm.; one-fourth of the square is equal to .0031 mm.; one-half of the square is equal to .0062 mm. Cell *D* is in the indirect division process. Cell *E* is a structure that is common among the tumor cells and I have concluded that it is a degeneration result, although it may occur anywhere in the cell nest among the otherwise vigorous cells. It is characterized by a large amount of deeply staining chromatic material, homogeneous and closely massed, having

no definite form but with a more or less regular outline. This mass evidently represents the nucleus, which has become filled with a diffused, swollen mass of chromatin. Its cell membrane has broken down, allowing the cytoplasm to flow out into the surrounding intercellular spaces. Notice the regular form of the chromatin nucleoli in this group of cells.

FIGURE 6. This group of eleven cells was drawn from the same cell nest as the previous group. Cell *A* is a large cell, .0093 mm. in its greatest diameter. In the cytoplasm about the nucleus are four vesicles, similar to those described under figures 2 and 4. The chromatin of its nucleus is of regular outline but is unusual on account of its size, being a trifle over one-half the diameter of the nucleus itself, at least twice the amount found in the ordinary resting cell. I think it is a cell just beginning the degeneration process shown by the swelling of its chromatin. Cell *C* is undoubtedly in the process of degeneration, for its cell membrane has disappeared, allowing the cytoplasm to flow out uncontrolled. It is a cell almost as large as cell *A*. Its chromatin, which exists as a deeply staining mass somewhat irregular in outline, was larger in diameter than that of cell *A*. The nuclear wall could not be made out. Cell *B* is one farther along in the process of breaking up than cell *C*, for most of its cytoplasm has gone. The diameter of its chromatic element is not so much larger than that of cell *C* but it is more condensed and of more regular outline. These three cells, I think, are respectively in advancing stages of disintegration. Cell *D* is a cell dividing indirectly, having a chromatic mass larger than that of cell *C* but of a looser arrangement, indicating individual chromosomes. It also maintains its cell borders perfectly.

FIGURE 7. This group of eleven cells was drawn from cell nest 6 in the region of a necrotic area. Cells *A* and *B* are in the fifth and sixth tiers respectively from the free edge of the tumor on the peripheral side of the group. I will use this group and the one following it, figure 8, to show changes in the cells passing inward from the free edge of the cell nest to a necrotic area. On the side peripheral to cell *A* there is a small necrotic spot two or three cells in diameter, which accounts for cells *A* and *B* on that side of the group. Cell *A* is a good specimen of such cells as *C* and *B* of figure 6 or cell *E* of figure 5. It shows the swelling of the chromatin and the disintegration of the cytoplasm well. While there has been a swelling of the chromatin in each of these cells there has been an equally great shrinkage of the nucleus, so that at this stage there has been a real loss of material to the nucleus. Cell *B* is peculiar in that its nucleus, while practically the same size as normal, stains very dark; not solid, as in *A*, but granular. There is also a faint indication of its chromatin nucleolus remaining, not indicating so much that it has become diffused through the karyoplasm as that the karyoplasm itself assumes a new staining power. The cell wall of cell *B* is broken down in one place, showing signs of disintegration. Cell *C*, a directly dividing cell, is .0093 mm. in its greatest diameter, while cell *D* is just a trifle less than .0125 mm. The average diameter of the resting cells of this group is near .007 mm. So I think that a cell preparing for direct division increases in size to a marked extent.

FIGURE 8. This group of sixteen cells is taken from cell nest 6, the same nest that group 7 is taken from, and drawn from a zone of cells to the inner side of group 7, that is, between group 7 and a necrotic core which lies in the central part of the nest. These two figures show well the transition from the more peripheral nondegenerating cells to the entirely necrotic mass of cell debris which fills the central portion of so many of the cell nests. No dividing cells were shown. Cell *A*, the most peripheral of the group, is the only one showing a chromatin nucleolus. It is an ordinary resting cell. In cells *B* and *B'*, a type of many cells found at this zone about the necrotic area, and for that reason described as characteristic, no chromatin nucleolus could be made out through the depth of the cell, but in each of these the chromatin was scattered through the karyoplasm in the form of a loose network, staining lightly. The cell and nuclear membranes were preserved perfectly. Passing inward toward the center of the nest is a field of cells which I have called "chromatic cells," and which are perfectly characteristic of a zone of cells that immediately surrounds the necrotic core of the cell nest. They are a transition stage between the normal cells and the wholly degenerated ones. They resemble closely the disintegrating cells described in figures 5, 6 and 7, but seem to have another history of formation. As in the other cells, the nucleus is filled with a homogeneous chromatic mass, the outer layers staining darker

than those farther toward the center. In this field the stain was not as intense as that in the cells of the previous figures but was of a grayish shade, and passing toward the necrotic area the light in the gray increases until in cells *D* and *D′* there is just enough black remaining to outline the nucleus well. From this stage it gradually fades out until the cells are entirely necrotic and do not stain at all. The cell membrane in this group could not be decided upon satisfactorily. In cells *A*, *B* and *B′* it was perfectly intact, while in cells *E* it seemed to be entirely gone. In other cells, as *C*, *C′*, the cell outline was definitely preserved, while yet again in cells *D* and *D′* the cell boundary was irregular and indefinite. But I am safe in saying that when the cell has so far degenerated that the color has disappeared from the nucleus the cell membrane has also disappeared and disintegration immediately follows. But in many of these cells the cell membrane has at least partially gone while the chromatin stains deeply. The nucleus of cell *B′* is 0.004 mm. in diameter while the chromatin mass of cell *C* is near 0.003 mm. in diameter, showing an appreciable shrinkage of this element in the degeneration process.

The Mitotic Divisions Occur in General Upon the Periphery of the Alveolus, the Amitotic Nearer the Center.

I will use camera lucida drawings, together with tables, to prove this. I counted the number of cells, the number of direct divisions and the number of indirect, and also counted the tier of cells from the periphery of the cell nest in which each division occurred. I hoped by this method to arrive at some conclusion as to the rapidity of growth of the tumor, in order to compare it later with the growth of the adult and embryonic mammary tissue. I also wished to decide as to the relative frequency in occurrence of the direct and indirect divisions and to note, if possible, whether there was any comparison between the relative proportions of these and the sort of nests in which they occurred. I also wished to decide if there was a well-founded relation between either of these methods of cell division and the necrotic areas indicating that one or the other was related to degeneration, or that they occurred equally in the same region showing that they were equally vital methods of cell growth.

Cell Nest 2 was the non-necrotic limb of a necrotic body. It was counted up to the beginning of the necrotic area. I cannot give the tiers of cells in which the various divisions occurred in this nest.

No. of cells.	*Direct divisions.*	*Indirect divisions.*
563	9	16

Percentage of cells in divisions	4.42
" of cells in direct divisions	1.50
" of cells in indirect divisions	2.90
" of divisions which are direct	36
" of divisions which are indirect	64

CELL NEST 3. This nest apparently is a small nest in diameter but it has four "chromatic cells," which indicates that it is somewhat degenerating.

Tier	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Av.*	*Total*
Direct D.	.	.	.	2	1	.	.	.	2	..	..	6.2	5
Indirect D.	3	1	.	1	1	.	.	.	.	..	..	2.3	6

No. of cells.	*Direct divisions.*	*Indirect divisions.*
253	5	6

Percentage of cells in divisions	4.34
" of cells in direct divisions	1.90
" of cells in indirect divisions	2.40
" of divisions which are direct	45.40
" of divisions which are indirect	54.50

CELL NEST 4. This was a nest with a necrotic center .125 mm. to .1125 mm. in diameter, while around this on the edge of the nest was a zone of cells varying in width from .05 mm. to .037 mm. which was undegenerate and which constituted the number of cells counted, so that the total number of cells counted does not show the real size of the nest in point of number of cells, one-half of the area of the nest being degenerate.

Tier	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Av.*	*Total*
Direct D.	1	.	3	1	2	1	1	1	.	1	1	5.5	12
Indirect D.	.	1	2	1	1	.	1	1	.	1	..	5.2	8

No. of cells.	*Direct divisions.*	*Indirect divisions.*
515	12	8

Percentage of cells in divisions	3.88
" of cells in direct divisions	2.30
" of cells in indirect divisions	1.50
" of divisions which are direct	60
" of divisions which are indirect	40

CELL NEST 5. This was one of the smaller sized nests and was quite vigorous, showing no degenerating cells at all.

Tier	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Av.*	*Total*
Direct D.	.	.	.	.	.	.	.	.	.	..	..	00	00
Indirect D.	3	.	.	1	.	.	.	.	.	..	..	1.7	4

No. of cells.	*Direct divisions.*	*Indirect divisions.*
106	00	4

Percentage	of cells in divisions	3.77
“	of cells in direct divisions	0
“	of cells in indirect divisions	3.77
“	of divisions which are direct	0
“	of divisions which are indirect	100

CELL NEST 6. This was a cross section of a large alveolus, being .2875 mm. in length and .1758 mm. in width. It was regularly oval in outline. There were two degenerate spots in it at opposite sides, the size of six to eight cells. With these exceptions the cells were all counted.

Tier	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Av.*	*Total*
Direct D.	.	1	4	1	.	3	.	2	1	..	..	5.0	12
Indirect D.	.	1	1	.	.	.	.	2	.	..	..	5.2	4

No. of cells.	*Direct divisions.*	*Indirect divisions.*
676	12	4

Percentage	of cells in divisions	2.36
“	of cells in direct divisions	1.70
“	of cells in indirect divisions	0.60
“	of divisions which are direct	75
“	of divisions which are indirect	25

CELL NEST 7. This was a small, oval, non-necrotic nest.

Tier	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Av.*	*Total*
Direct D.	.	.	.	.	.	.	.	.	.	..	..	00	00
Indirect D.	1	4	.	.	.	.	.	.	.	..	..	1.8	5

No. of cells.	*Direct divisions.*	*Indirect divisions.*
123	00	5

Percentage	of cells in divisions	4.06
“	of cells in direct divisions	0
“	of cells in indirect divisions	4.06
“	of divisions which are direct	0
“	of divisions which are indirect	100

CELL NEST 9. This was a large necrotic nest, .2125 mm. in diameter, with a necrotic center .1125 mm. in diameter, which had a border of vigorous cells .05 mm. wide.

Tier	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Av.*	*Total*
Direct D.	1	.	4	.	1	1	.	.	.	1	..	4.2	8
Indirect D.	1	.	1	.	.	.	.	.	.	..	..	2.0	2

No. of cells.	*Direct divisions.*	*Indirect divisions.*
299	8	2

Percentage	of cells in divisions	3.34
“	of cells in direct divisions	2.60
“	of cells in indirect divisions	0.70
“	of divisions which are direct	80
“	of divisions which are indirect	20

In the following cell nests I have taken the serial sections of the same nest and counted them in the same way as I did the single sections of the previously counted nests. I hope in this way to in a manner corroborate my results and also to study the history of the cell nest farther.

CELL NEST 10. This nest was .4125 mm. in length, .0875 mm. in width. It was a nest that showed occasional spots of six to eight cells that had broken down, an average of two of these spots in each nest. The direct divisions occurred largely in the upper, wider end, while the indirect occurred largely in the lower, narrower end, but I have not illustrated this by sketches. It was therefore taken as a nest, non-necrotic, but near the stage when it would rapidly have become so, indicated by the degenerate spots.

CELL NEST 10, A.

Tier.	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Av.*	*D.D.*	*I.D.*	*Cells.*
Direct D.	.	.	1	2	1	2	1	.	.	1	..	5.6	8	..	...
Indirect D.	1	6	2	3	.	2	.	.	.	..	..	3.0	..	14	532
CELL NEST 10, B.															
Direct D.	1	1	2	5	1	2	.	.	.	..	..	4.2	12	..	...
Indirect D.	2	3	3	3	.	.	.	.	.	..	..	2.6	..	11	600
CELL NEST 10, C.															
Direct D.	.	3	1	.	.	3	.	.	.	..	..	3.8	7	..	...
Indirect D.	2	2	.	3	2	.	.	.	.	..	..	3.1	..	9	557
CELL NEST 10, D.															
Direct D.	.	1	1	3	2	2	1	.	.	..	..	4.6	10	..	...
Indirect D.	2	3	2	2	.	.	.	.	.	..	..	2.4	..	9	655
CELL NEST 10, E.															
Direct D.	.	.	3	2	2	1	1	.	.	..	..	4.4	9	..	...
Indirect D.	1	1	2	1	1	1	.	.	.	..	..	3.4	..	7	654
CELL NEST 10, F.															
Direct D.	.	.	4	3	2	2	.	.	.	..	..	4.1	11	..	...
Indirect D.	2	2	3	4	.	2	1	.	.	..	..	3.5	..	14	650
CELL NEST 10, G.															
Direct D.	.	.	1	.	.	4	2	.	.	..	..	5.8	7	..	...
Indirect D.	3	7	2	1	.	1	1	.	.	..	..	2.6	..	15	564

No. of cells.	*Direct divisions.*	*Indirect divisions.*
4212	64	79

Percentage of cells in divisions	3.39
" of cells in direct divisions	1.50
" of cells in indirect divisions	1.80
" of divisions which are direct	44
" of divisions which are indirect	56

The direct divisions averaged 1.68 rows nearer the center than the indirect divisions.

Cell Nest 11. This nest was probably one-half of a half necrotic alveolus. A sketch of it in cell nest 11 *A* is given in figure 9. The cross-hatched area shows that part of the nest that is necrotic, while the white border about it is the area of the cells counted.

Tier.	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Av.*	*D.D.*	*I.D.*	*Cells.*
Cell Nest 11, A.															
Direct D.	.	2	.	1	.	.	.	.	.	..	..	2.6	3	..	...
Indirect D.	.	1	.	2	.	.	.	.	.	..	..	3.3	..	3	334
Cell Nest 11, B.															
Direct D.	.	3	.	1	.	3	.	1	.	1	..	5.1	9	..	...
Indirect D.	2	.	1	.	.	.	.	.	.	..	..	1.6	..	3	305
Cell Nest 11, C.															
Direct D.	.	.	.	1	1	3	.	1	.	..	..	5.8	6	..	...
Indirect D.	1	4	.	1	.	1	.	.	.	..	..	2.7	..	7	279
Cell Nest 11, D.															
Direct D.	1	.	2	1	1	2	1	.	.	..	..	4.3	8	..	...
Indirect D.	1	2	1	.	.	.	.	.	.	..	..	2.0	..	4	296
Cell Nest 11, E.															
Direct D.	.	1	1	.	2	.	.	.	1	.	..	4.8	5	..	...
Indirect D.	1	1	.	1	1	.	.	.	.	..	..	3.0	..	4	279
Cell Nest 11, F.															
Direct D.	.	.	1	.	1	.	1	.	.	1	..	6.2	4	..	...
Indirect D.	2	.	2	.	.	3	.	.	.	..	..	3.7	..	7	271
Cell Nest 11, G.															
Direct D.	.	2	1	1	3	.	.	1	1	1	..	5.3	10	..	...
Indirect D.	3	1	.	.	1	.	.	.	.	..	..	2.0	..	5	404
Cell Nest 11, H.															
Direct D.	.	2	2	1	.	.	1	.	1	..	..	4.2	7	..	...
Indirect D.	.	3	1	1	1	.	.	.	.	..	..	3.0	..	6	391
Cell Nest 11, I.															
Direct D.	.	.	2	.	2	2	.	.	1	1	..	5.8	8	..	...
Indirect D.	.	3	1	2	2	.	1	.	.	..	..	3.6	..	9	393
Cell Nest 11, J.															
Direct D.	.	1	.	.	.	.	2	.	.	..	..	5.3	3	..	...
Indirect D.	1	.	1	3	1	.	.	.	.	..	..	3.5	..	6	306

No. of cells.	*Direct divisions.*	*Indirect divisions.*
3258	63	54

Percentage of cells in divisions	3.59
" of cells in direct divisions	1.90
" of cells in indirect divisions	1.60
" of divisions which are direct	53.80
" of divisions which are indirect	46.10

The direct divisions in this nest averaged 2.1 rows farther away from the free edge of the nest than the indirect, or 2.1 rows nearer the center of the nest.

CELL NEST 8. The work upon this nest was done with greater care than that upon the previous nests. I first made a camera lucida sketch of the nest in outline, then went over the nest carefully with the high power 8x compensating ocular and marked each division I found upon the outlined sketch. I then used an 8x Huyghenian ocular, upon the diaphragm of which I had placed a micromillimeter scale, and went over the field again, carefully counting the cells by the aid of the micrometer scale, and verified the previous locations of the dividing cells and located any new ones that I may have missed in the first survey. I thus corroborated my work and made it doubly sure by locating each dividing cell upon an outline sketch. I also used these sketches in the hope that together with the tables I might farther establish the apparent relation of directly dividing cells to the degenerating areas. Where this relation has been especially noticeable I have made high-power camera lucida drawings of the particular field to show some detail about the cells I counted, simply drawing the more important structures in relation to them. Using these large drawings and marking their position upon the smaller sketches one cannot avoid showing in the same way the slide does the real relation of the various dividing cells to these necrotic areas. In these outline sketches I only outlined the nest, tracing into any irregularities among the cells along the edge, so that, unless otherwise marked, rifts in the nests will mean spaces left where the cells have apparently been pulled apart by external means. The areas that are entirely necrotic will not be distinguished from those that show definite degenerating changes; cells that are in the "chromatic cell" stage I have counted as necrotic. These areas are shown by cross-hatched work. The indirect divisions are shown by a dot or "×" while the direct divisions are shown by a circle. Starting with figure 10 the sections are in serial arrangement. This cell nest 8 is only a portion of the entire alveolus, showing at the right side of the sketch just the end of a necrotic plug, and leaving the greater part shown in the vigorous condition. I used this nest to contrast, if possible, the two divisions in these two areas.

FIG. 10. CELL NEST 8, A.

Tier.	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Av.*	*D.D.*	*I.D.*	*Cells.*
Direct D.	.	1	.	1	3	.	.	2	1	..	..	5.4	8	..	...
Indirect D.	2	4	4	1	2	2	.	.	.	..	..	3.2	..	15	534
FIG. 11. CELL NEST 8, B.															
Direct D.	.	1	2	3	2	.	1	.	.	..	..	4.1	9	..	...
Indirect D.	1	4	4	3	1	2	.	.	.	..	..	3.3	..	15	511
FIG. 12. CELL NEST 8, C′.															
Direct D.	.	1	1	1	5	1	3	2	1	..	..	5.7	15	..	...
Indirect D.	7	3	3	3	2	1	4	1	.	..	..	3.5	..	24	554
FIG. 14. CELL NEST 8, C.															
Direct D.	.	1	2	2	2	2	.	1	.	..	..	4.6	10	..	...
Indirect D.	2	2	2	5	2	1	1	1	.	..	..	4.0	..	16	555
CELL NEST 8, D.															
Direct D.	1	2	.	1	2	3	2	.	.	..	..	5.1	11	..	...
Indirect D.	3	1	3	3	4	1	1	.	.	..	..	3.6	..	16	626
SUBNEST 8, D.															
Direct D.	.	.	.	1	1	.	.	.	.	..	..	4.5	2	..	...
Indirect D.	3	5	1	.	.	.	.	.	.	..	..	1.7	..	9	172
CELL NEST 8, E.															
Direct D.	.	1	2	2	3	2	.	.	.	..	1	4.9	11	..	...
Indirect D.	4	3	7	4	4	.	.	.	.	..	..	3.0	..	22	869
CELL NEST 8, F.															
Direct D.	.	.	3	2	6	2	3	.	.	..	..	5.0	16	..	...
Indirect D.	3	5	3	2	2	2	.	.	.	..	..	3.0	..	17	745
FIG. 16. CELL NEST 8, G.															
Direct D.	.	2	3	1	3	4	1	1	.	..	..	4.7	15	..	...
Indirect D.	2	6	2	1	.	1	1	.	.	..	..	2.8	..	13	916
FIG. 18. CELL NEST 8, H.															
Direct D.	1	2	3	1	.	3	3	.	.	..	..	4.3	13	..	...
Indirect D.	3	1	7	1	.	.	2	.	1	..	..	3.5	..	15	907
FIG. 19. CELL NEST 8, I.															
Direct D.	1	.	2	1	2	.	1	3	.	..	1	5.7	11	..	...
Indirect D.	1	1	7	2	4	1	1	.	.	..	..	3.8	..	17	912

No. of cells.	*Direct divisions.*	*Indirect divisions.*
7301	121	179

Percentage of cells in division	4.01
" of cells in direct division	1.60
" of cells in indirect division	2.40
" of divisions which are direct	40.33
" of divisions which are indirect	59.66

The direct divisions of this nest averaged 1.78 rows nearer the center than the indirect.

DESCRIPTION OF OUTLINE SKETCHES AND DRAWINGS.

CELL NEST 8, "A" (fig. 10). The amount of necrotic material in this figure is greater than in the following ones, the necrotic plug showing less and less in each consecutive section. There are no divisions shown in this figure near the necrotic plug, but the nearest two are direct. The greater part of the dividing cells are in the limb of the nest.

CELL NEST 8, "B" (fig. 11). The number of divisions present in the distal part of the limb is noticeable. There are three direct divisions immediately adjacent to the necrotic plug and one nearer than the nearest indirect division.

CELL NEST 8, "C" (fig. 12). In this nest there was an unusually large number of dividing cells. At the point of the arrow in figure 12 is the center of the group of cells drawn on a large scale in figure 13. About the arrow point are the four direct divisions and the two indirect divisions shown in the enlarged group. This group of nineteen cells includes a larger area under the lens than any previously drawn. I drew all the cells of importance under the field of the camera lucida, including a field .05 mm. in diameter, while the previous groups drawn have included an area only .0375 mm. in diameter. It is located on the edge of the necrotic area and includes the whole width of cells lying between this area and the free edge of the cell nest, cell *F* being in the first row of the nest, while cell *B* is among the necrotic cells. The direct divisions of this section are deep in the center of the nest, while the indirect are largely very close to the edge, seven cells out of twenty-five dividing indirectly lying in the first row and no directly dividing cells nearer than the second row, and then only one. A general survey of these sketches together with the tables strongly indicates that the cells on the edge of the tumor increase almost, if not wholly, by indirect divisions, while those deeper away from the edge increase largely by direct divisions but occasionally by indirect. I want to emphasize by the large drawings the intimate association of the directly dividing cells with the degenerate ones. Cells *H*, *H′*, *H″* are the "chromatic cells" that I have described previously under figure 13. Surrounding these cells closely are cells *A*, *B*, *C*, *D* and *E*, plainly in the process of direct division. Cell *B* is peculiar in that it shows no chromatin nucleolus in either segment of the nucleus. This same occurrence was noticed in numbers of resting cells, *B*, *B′*, figure 8, etc., just outside the zone of "chromatic cells" *H*, *H′*, *H″*. Its chromatin had wholly or largely disappeared, and if any remained it was loosely diffused through the karyoplasm. Cell *E* is another cell showing no chromatin in any of the segments of its nucleus. It evidently was in decay for it was very translucent. The fragments of its nucleus showed no chromatin at all. It may be that a cell such as *B*, which has vigor enough to cause its nucleus to segment but not to cytoplasm, gradually loses its staining ability and its definiteness of outline and later becomes merely a mass of debris through a stage represented in cell *E*. Cells *F* and *G* are two cells in the indirect division process. The directly dividing cells are much larger than the resting cells or those dividing indirectly. Cell *A* is .0093 mm. in its greatest diameter, cell *B* is .007 mm., cell *C* is .0093 mm., cell *G* is .0062 mm., cell *F* is .0062 mm., cell *E* is .0093 mm., cell *D* is .0085 mm., while cell *I*, an average resting cell, is .0062 mm. in its greatest diameter. This cell shows the breaking up of the chromatin and its diffusion through the karyoplasm, possibly preceding cells *H*, *H′*, *H″*. Its nucleus is .005 mm. in diameter, while the diameter of the "chromatic mass" in cells *H*, *H′*, *H″* is .0031 mm., showing evidently a shrinkage in the latter.

FIGURE 14. In this section two indirect divisions are shown located on the very edge of the necrotic plug, and two more near. There are also close to the edge of the nest three direct divisions, still showing a greater proportion of direct divisions near the necrotic area than indirect, when compared with the total number of divisions of each in the section. But this shows that indirect division may occur on the very edge of a degenerating area.

At the lower extremity of the limb of the regular section following is found a circular group of cells, which in the next section shows a connection with the larger body. This is the first appearance of this group, but in the previous sections there is a circular space indicating where it has been but from which it has in some way been lost. There is a cleft entirely through the regular section, but this was where the cells had pulled apart and not where they had degenerated. The direct divisions are intimately associated with the necrotic spots. In the middle segment there are two indirect divisions on the edge of the necrotic area, but usually they are near the free edge of the nest.

In the succeeding section the subnest has joined the limb of the main body and it was all counted together. There are three necrotic areas in this section. In the lower one the two directly dividing cells of that region are on the edge of the degenerated area.

A later section shows the nest in two segments, broken apart from each other. A pluripolar cell division shows at one place.

The group of cells drawn under high power in figure 15 is from this section. Figure 15 shows a group of five directly and one indirectly dividing cells. In this drawing and those made hereafter I shall indicate the segments of the nucleus as they appear through the depth of the cell, demonstrating their overlapping. The border line used was drawn at the edge of the cells which presented no marked degeneration changes, but it is not a hard, fast line, a few vigorous cells jutting out farther than the line and a few chromatic cells being behind it. Cells *A, B, C, D* and *E* show well-marked direct divisions. Cell *A* is on the necrotic border. Cell *B,* a very small cell for a directly dividing one, is a half cell width from the necrotic border. Cell *C* is a trifle closer than *B* to the border. Cell *D* is in the third row from the border. It is peculiar in that its chromatin nucleoli in each segment are not staining deeply and the chromatin is diffused through the karyoplasm. Cell *E* is in the fourth row from the necrotic edge. Cell *F* is an indirectly dividing cell and is in the same row of cells as cells *C* and *B*. Cells *G* and *G′* are the "chromatic cells" described under figure 13. They mark the edge of the necrotic plug and are in various stages of degeneration, as indicated by the disintegration of their cytoplasm and the loss of the staining power of their chromatin. This sketch together with the smaller one shows well this collecting of large numbers of the directly dividing cells about these necrotic areas. There are mitotic cells here, but not in such proportion in comparison to their total number as the amitotic.

FIGURE 16. In this section there are more direct divisions than indirect. There is a noticeable change in the number of indirect divisions in the lower part of the nest, in what was termed a "subnest" in a preceding section. In one section there are nine indirect divisions, two direct. In the next there

are eight indirect divisions, two direct. In the next there are five indirect divisions, three direct. In a later (fig. 16), there are five indirect divisions, four direct. In another (fig. 19), there are four indirect divisions, three direct. This shows consistently in this case that as the center of the nest is approached in the sections the number of direct divisions increase in proportion while the indirect decrease in proportion. In the region of the arrow point of figure 16 an enlarged drawing was made (figure 17). I used this to show more detail about the cells shown in figure 16. Cell *A* was on the edge of the necrotic area. Its chromatin was small in amount and gathered in two clumps in one segment and three in the other. Cell *C* is an ordinary dividing cell. Cell *D* is in the second row from the necrotic edge. The cross-hatched work shows the necrotic area, this area being entirely necrotic and showing no transition cells along the edge.

FIGURE 18. There are but two dividing cells in the upper segment of this nest, while in an earlier there are fourteen, the number decreasing with each section until this one. They have increased steadily in the middle part of the limb, however, from eleven to nearly twenty in the section shown in figure 18. This carefully worked out will demonstrate that at the same time the cells in one part of the nest are rapidly dividing those in another part are not dividing at all. There is either an unequal stimulus to growth in the nest or an unequal negative cause.

FIGURE 19. This nest is the same one as that in the preceding figure, but in this section the two parts have been separated. At the point of the arrow is the location of figure 20, and here are shown the three dividing cells drawn in figure 20. In figure 20, cell *A* is plainly among the degenerating cells in the necrotic plug, and is surrounded by "chromatic cells," no vigorous cell being near. It is a large clear cell with a bisegmented nucleus and showing but very little chromatin. Its appearance indicates that it is a degenerating cell. Cell *B* lies just outside the border of vigorous cells. Its nucleus is bisegmented and it stains much deeper than the cytoplasm. The chromatin nucleoli stain very faintly. Cell *C* is a large clear cell lying in the third row of cells from the necrotic edge. It stains lighter than the other cells about it and shows a small amount of chromatin and that stained faintly. Cells *A* and *B*

are noticeable because they have broken off from the vigorous growth and lie among cells that are distinctly necrotic.

Out of the 294 direct divisions in all the nests only 7 occurred in the first row on the edge of the nest.

Out of the 357 indirectly dividing cells 63 occurred in the first row on the edge of the nest.

The direct divisions in all the nests averaged 1.68 rows nearer the center than the indirect divisions.

CELL NEST 12. This nest was sketched and counted in forty-two serial sections. It began as three or four groups of cells which were the cross sections of limbs which later fused into a common trunk. It was non-necrotic throughout.

CELL NEST 12, I.

Tier	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*Av.*	*D.D.*	*I.D.*	*Cells*
Direct D.	.	.	1	.	.	.	.	3.0	1	..	...
Indirect D.	2	1	4	.	.	.	.	2.2	.	7	166

CELL NEST 12, II.

Direct D.	.	.	.	.	.	.	.	..	.	..	...
Indirect D.	.	4	.	1	1	.	.	2.8	.	6	140

CELL NEST 12, III.

Direct D.	.	2	.	.	.	.	.	2.0	2	..	...
Indirect D.	.	1	.	.	.	.	.	2.0	.	1	78

CELL NEST 12, IV.

Direct D.	.	.	1	.	.	.	.	3.0	1	..	...
Indirect D.	2	.	.	1	.	.	.	2.0	.	3	77

CELL NEST 12, V.

Direct D.	.	.	.	.	.	.	.	..	.	..	...
Indirect D.	2	3	1	.	.	.	.	1.8	.	6	180

CELL NEST 12, VI.

Direct D.	.	.	1	.	.	.	.	3.0	1	..	...
Indirect D.	.	1	1	.	.	.	.	2.5	.	2	81

CELL NEST 12, VII.

Direct D.	.	1	1	.	.	.	.	2.5	2	..	...
Indirect D.	.	.	2	1	.	.	.	2.3	.	4	85

CELL NEST 12, VIII.

Direct D.	.	.	.	.	.	.	.	..	.	..	...
Indirect D.	1	3	.	3	.	.	.	2.7	.	7	83

CELL NEST 12, IX.

Direct D.	.	.	1	1	.	.	.	3.5	2	..	...
Indirect D.	1	1	1	.	.	.	.	2.0	.	3	86

CELL NEST 12, X.

Direct D.	.	.	.	2	.	.	.	4.0	2	..	...
Indirect D.	2	2	.	.	.	.	.	1.4	.	4	169

CELL NEST 12, XI.											
Direct D.	.	.	.	.	.	.	.	..	.	..	...
Indirect D.	3	3	2	.	.	.	.	1.9	.	8	206
CELL NEST 12, XII.											
Direct D.	.	.	.	.	.	.	.	..	.	..	...
Indirect D.	2	2	2	.	.	.	.	2.0	.	6	227
CELL NEST 12, XIII.											
Direct D.	1	1	.	.	3	.	.	3.6	5	..	...
Indirect D.	6	1	.	.	.	.	.	1.1	.	7	235
CELL NEST 12, XIV.											
Direct D.	.	.	.	4	.	.	.	4.0	1	..	...
Indirect D.	5	.	2	.	.	.	.	1.5	.	7	360
CELL NEST 12, XV.											
Direct D.	.	.	.	.	1	.	.	5.0	1	..	...
Indirect D.	3	.	2	.	1	1	.	2.8	.	7	328
CELL NEST 12, XVI.											
Direct D.	.	.	.	1	.	.	.	4.0	1	..	...
Indirect D.	3	.	1	1	2	1	.	3.2	.	8	335
CELL NEST 12, XVII.											
Direct D.	.	.	1	1	.	.	.	3.5	2	..	...
Indirect D.	4	2	1	1	.	.	.	1.9	.	8	365
CELL NEST 12, XVIII.											
Direct D.	.	.	.	1	.	.	.	4.0	1	..	...
Indirect D.	9	.	2	.	1	.	.	1.6	.	12	362
CELL NEST 12, XIX.											
Direct D.	.	.	.	.	1	1	.	5.5	2	..	...
Indirect D.	5	.	.	.	.	1	.	1.6	6	..	309
CELL NEST 12, XX.											
Direct D.	.	.	1	.	.	1	.	4.5	2	..	...
Indirect D.	1	3	.	1	.	1	.	2.5	.	6	332
CELL NEST 12, XXI.											
Direct D.	.	2	.	.	.	.	.	2.0	1	..	...
Indirect D.	2	1	.	.	.	.	.	1.3	.	3	215
CELL NEST 12, XXII.											
Direct D.	.	.	.	.	.	.	.	..	.	..	...
Indirect D.	1	4	1	1	.	.	.	2.4	.	7	209
CELL NEST 12, XXIII.											
Direct D.	1	1	.	1	1	.	.	3.0	4	..	...
Indirect D.	2	.	2	.	.	.	.	2.0	.	4	254
CELL NEST 12, XXIV.											
Direct D.	.	1	.	.	.	.	.	2.0	1	..	...
Indirect D.	6	1	2	.	.	.	.	1.5	.	9	288
CELL NEST 12, XXV.											
Direct D.	.	.	.	.	1	.	.	5.0	1	..	...
Indirect D.	2	3	.	.	.	.	.	1.7	.	5	449

Cell Nest 12, XXVI.

Direct D.	.	.	1	1	.	1	.	4.3	3	..	...
Indirect D.	5	4	.	.	.	.	.	1.4	.	9	316

Cell Nest 12, XXVII.

Direct D.	.	1	2	.	.	1	.	3.5	4	..	...
Indirect D.	6	3	2	.	.	.	.	1.6	.	11	230

Cell Nest 12, XXVIII.

Direct D.	.	1	1	2	.	.	.	3.2	4	..	...
Indirect D.	3	2	1	1	1	.	.	2.4	.	8	334

Cell Nest 12, XXIX.

Direct D.	.	1	.	.	.	.	.	2.0	1	..	...
Indirect D.	3	.	2	2	.	.	.	2.4	.	7	293

Cell Nest 12, XXX.

Direct D.	.	.	2	.	.	.	.	3.0	2	..	...
Indirect D.	5	2	1	.	.	.	.	1.5	.	8	307

Cell Nest 12, XXXI.

Direct D.	1	.	.	.	.	.	.	1.0	1	..	...
Indirect D.	3	2	1	.	.	.	.	1.6	.	6	334

Cell Nest 12, XXXII.

Direct D.	.	1	.	.	.	1	.	4.0	2	..	...
Indirect D.	1	2	1	.	.	.	.	2.0	.	4	281

Cell Nest 12, XXXIII.

Direct D.	1	.	.	.	1	1	.	4.0	3	..	...
Indirect D.	5	1	1	.	.	.	.	1.4	.	7	435

Cell Nest 12, XXXIV.

Direct D.	1	1	.	.	1	.	.	2.6	3	..	...
Indirect D.	2	.	1	.	1	.	.	2.5	.	4	381

Cell Nest 12, XXXV.

Direct D.	.	1	.	.	.	2	.	4.6	3	..	...
Indirect D.	5	2	.	.	1	.	.	1.7	.	8	431

Cell Nest 12, XXXVI.

Direct D.	.	.	.	.	1	1	.	5.5	2	..	...
Indirect D.	4	3	1	2	.	.	.	2.1	.	10	479

Cell Nest 12, XXXVII.

Direct D.	.	3	.	1	.	.	.	2.5	4	..	...
Indirect D.	3	6	1	1	.	.	.	2.0	.	11	537

Cell Nest 12, XXXVIII.

Direct D.	.	1	.	.	.	1	.	4.0	2	..	...
Indirect D.	6	2	1	1	.	.	.	1.7	.	10	551

Cell Nest 12, XXXIX.

Direct D.	1	.	.	3	.	1	1	4.3	6	..	...
Indirect D.	5	4	1	1	.	.	.	1.8	.	11	498

Cell Nest 12, XL.

Direct D.	.	.	.	.	2	.	.	5.0	2	..	...
Indirect D	6	2	2	.	.	.	.	1.6	.	10	410

CELL NEST 12, XLI.

Direct D.	.	2	.	.	.	.	.	2.0	2	..	...
Indirect D.	2	.	.	.	.	.	3	4.6	.	5	371

CELL NEST 12, XLII.

Direct D.	.	1	1	.	.	2	.	4.2	4	..	...
Indirect D.	4	2	3	.	.	1	.	2.3	.	10	421

No. of cells.	*Direct divisions.*	*Indirect divisions.*
12,228	81	285

Percentage of cells in divisions	2.99
" of cells in direct divisions	.6
" of cells in indirect divisions	2.3
" of divisions which are direct	22.1
" of divisions which are indirect	77.9

Table of all the nests counted, showing percentage of cells in division, percentage of cells in direct division, and percentage of cells in indirect division:

Cell nest.	*Percentage of cells in division.*	*Percentage of cells in direct division.*	*Percentage of cells in indirect division.*
2	4.42	1.5	2.9
3	4.34	1.9	2.4
4	3.88	2.3	1.5
5	3.77	0.0	3.77
6	2.36	1.7	.6
7	4.06	0.0	4.06
8	4.01	1.6	2.4
9	3.34	2.6	.7
10	3.39	1.5	1.8
11	3.59	1.9	1.6
12	2.99	.6	2.3

The writer of this paper wishes here to acknowledge his indebtedness to Doctor McClung, whose kind suggestions made this work possible, and to Doctor M. T. Sudler for the material and clinical data upon which this study is based.

CONCLUSIONS.

1. The percentage of cells in division shows no relation to the percentage of amitoses or mitoses.

2. The percentage of mitoses is high in small non-necrotic nests.

3. The percentage of amitoses is high in large necrotic nests, indicating that it is the division associated with degeneration.

4. Amitosis is the form of division occurring in the necrotic area.

5. The rate of division in the various nests is inconstant.

6. The directly dividing cells lie nearer the center of the cell

nests and thus nearer the necrotic areas than the indirectly dividing cells.

7. The indirectly dividing cells lie nearer the periphery of the nest than the directly dividing cells.

8. From these observations it may therefore reasonably be concluded that amitosis represents the final effort of the cell at reproduction, and that shortly after its occurrence degeneration ensues.

9. Amitosis, mitosis and disintegration comprise the cell changes in the alveoli.

10. Cells in direct and indirect division are larger than the resting cells.

11. In one stage of degeneration of the cells the chromatin becomes diffused through the karyoplasm and so swells that it fills the nucleus as a deeply staining, homogeneous mass. In another process of degeneration the chromatin loses its staining power and the cell becomes clear.

12. There is a shrinkage of the nuclear bulk in degeneration.

13. A border of chromatic cells lies between the vigorous cells and the cell debris of the necrotic area and marks the limit of degeneration; such cells are themselves degeneration results.

BIBLIOGRAPHY.

C. M. Child. Studies on the Relation Between Amitosis and Mitosis. Biological Bulletin, vol. XII, No. 2, January, 1907.

J. George Adami. General Pathology.

J. E. S. Moore and C. E. Walker. First Report on the Cytological Investigation of Cancer, 1906.

Alfred Stengel. General Pathology.

J. T. Patterson. Amitosis in the Pigeon's Egg. Anatomischer Anzeiger, Bd. 32, 1908.

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CONTENTS:

THE TEMNOSPONDYLOUS AMPHIBIA AND A NEW SPECIES OF ERYOPS FROM THE PERMIAN OF OKLAHOMA, . . . *Roy L. Moodie.*

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THE KANSAS UNIVERSITY SCIENCE BULLETIN.

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THE TEMNOSPONDYLOUS AMPHIBIA AND A NEW SPECIES OF *ERYOPS* FROM THE PERMIAN OF OKLAHOMA.

BY ROY L. MOODIE.

(Contribution from the Zoölogical Laboratory, No. 189.)

Plates XLIX to LIV.

OUR knowledge of the fossil Amphibia begins with Dr. J. J. Scheuczer's discovery of two skeletons in the Miocene of Oeningen, which he referred to as "*Homo diluvii testis et Theoskopos,*" and which later Hermann von Meyer designated "*Andrias scheuczeri,*" thus keeping the same idea in the generic name as Scheuczer had expressed in his letters and descriptions. The discovery was made about 1725, so far as I can ascertain. His letter to Sir Hans Sloane in 1726, which was translated in the republished volume of the early transactions of the Royal Society of London, is the first definite mention I find of this discovery in the literature which is accessible to me.

Exactly one hundred years elapsed from the time of Scheuczer's discovery of the giant salamander skeletons to the time when Dr. Georg Friedrick Jaeger discovered in the Triassic of Germany some labyrinthodont remains which he figured and described in his folio published in 1824 at Stuttgart with the title "De Ichthyosauri sive Proteosauri Fossilis Specimenibus in Agro Bollensi in Wurtembergia." He figured the occipital portion of the skull and teeth of what he, in 1828, called "Mastodonsaurus." In 1833 Doctor Jaeger pointed out the synonymy of *Salamandroides* with *Mastodonsaurus*. Previous to

Doctor Jaeger's discovery, however, was that of the form *Pygopterus,* the history of which is given below.

The literature on fossil Amphibia for the next twenty years following Jaeger's last mentioned paper deals almost entirely with the Tertiary Amphibia, although in 1844 and 1845 Hermann von Meyer published some interesting papers on the more ancient amphibians. It is interesting to note that in von Meyer's "System der fossilen Saurier," 1845, he does not mention a single temnospondylous amphibian.

Our knowledge of the Temnospondylia dates from the year 1847, in which year Dr. August Goldfuss described *Archegosaurus,* the first known and for many years the only representative of this order of amphibians. Doctor Goldfuss gave as the title of the paper in which he described *Archegosaurus* "Ueber das ælteste der mit Bestimmtheit erkannten Reptilien." It will thus be noticed from the literature that the early writers regarded the labyrinthodonts and their allies as reptiles. It was Quenstedt who in 1850 made the first contention that "Die Mastodonsaurier im gruenen Keuper Sandstein Wurtemburgs sind Batrachier," and from that time dates the development of our knowledge of these extinct forms as Amphibia. Three years after Quenstedt's paper appeared, Vogt upheld the same contention in his essay "Archegosaurus und all Labyrinthodonten sind Amphibien nicht Reptilien."

In 1850, after the discovery of the *Archegosaurus* and its identification, Doctor Jaeger published an interesting essay entitled "Ueber die Uebereinstimmung des *Pygopterus lucius* Ag. mit dem *Archegosaurus dechenii* Goldf." In this essay Jaeger brings out the interesting facts of the early discovery of the *Archegosaurus.* I give the following translation of the first paragraph of Jaeger's essay: "In the collection of the late Professor Storr, of Tübingen, which was received in 1817 at the Imperial Museum of Natural History at Stuttgart, there was found a skull enclosed in a spherosiderite nodule. This skull was listed in 1777 as No. 192, in the printed catalogue of the Pasquay collection (which was the foundation of the Storr collection), without giving the locality, as a fish skull which had been discovered in a non-fissile gray shale. Agassiz, at whose disposal the entire collection of fossil fishes was soon after placed, designated this specimen on a label in his own handwriting at first as *Aspidorhynchus* nov. sp. On a label written by him later it is designated as *Pygopterus lucius*. In the first part of the second volume of the Fossil Fishes (Poissons fossiles), page 10, Agassiz placed this skull in the family Sauroidæ as the second species of the genus *Pygopterus*, with the short description: '*Pygopterus lucius* Ag., une tête seulement, dont la mâchoire supérieure est plus allongée. Houille de Saarbrück.' In the same work, part II, page 78, this specimen is designated as the fifth species of *Pygopterus*, with the description, 'une tête avec des dents très acerées, de la houille de Saarbrück. L'original se trouve au Musée de Stuttgart.' He regards the same specimen as the third species on page 162 in the synoptic table of the family Sauroidæ arranged in the order of the formations of the Carboniferous which contained Sauroidæ. It is also given this place in the general table of fossil fishes which appeared in 1844, page xxxvi."

Jaeger affirmed the supposition of Agassiz that the specimen was from Saarbrück, from the similarity of the nodule to those found at that place. He then proceeded to show that the skull described by Agassiz as *Pygopterus lucius* really shows reptilian characters which Jaeger regarded as intermediate between those of a crocodile and an *Iguana*. He then compared it with the skull of a young crocodile and also with the skulls of various lizards. He found that the measurements and proportions of the skull compare favorably with those of the crocodile, and that the teeth have the form and size of those of a newly born crocodile. The position of the orbit is also identical with that of the crocodile. He made the important observation that the nostrils have the lateral position of the lizards. He then compared the specimen with other known fossil forms, *i. e.*, *Zygosaurus*, *Rhinosaurus* and the labyrinthodonts, and found considerable differences. He then made the following interesting observations regarding *Archegosaurus:* "At the meeting of naturalists in Aachen in 1847 Goldfuss described the remains in one of the many spherosiderite nodules, which contained a reptile skull, to which he gave the name *Archegosaurus*. He established three species for the genus, which he described more fully in a later publication. Only one species of this genus, *Archegosaurus decheni*, was described and figured in the Neues Jahrbuch für Mineralogie, 1847, Tab. VI, with a line drawing." Jaeger then pointed out in a conclusive manner the identity of *Pygopterus lucius* with *Archegosaurus*. He regarded *Archegosaurus* as allied to the Crocodilia but having characters of the Batrachia as were exhibited in the labyrinthodonts, and on account of the geological position of the fossils he supposed that *Archegosaurus* would really belong with the labyrinthodonts.

Huxley in 1862 described *Pholidogaster pisciformis* from the Carboniferous of Scotland. In the next year he distributed the ancient Amphibia into the two groups, the Archegosauria and the Mastodonsauria of von Meyer. In the former group he placed *Pholidogaster,* to which it manifestly does not belong. Huxley was himself doubtful as to its location, for he says: "*Archegosaurus,* of course, takes its place among the Archegosauria; and *Pholidogaster,* I suspect, must go with it, though its vertebræ are far better ossified"; and in a footnote he makes the interesting statement: "It seems to me probable that the vertebral centra of *Archegosaurus* may really have been osseous rings, such as are found in embryo frogs and salamanders," which shows that he was on the right track but did not quite comprehend the nature of the vertebræ of *Archegosaurus.*

Our knowledge for the next few years of our history is advanced but little, and that only by sundry discussions on *Archegosaurus.* In 1866 Owen placed *Archegosaurus* in his subclass "Dipnoa," under the order "Ganocephala." In the same year Haekel retained Owen's classification, except that he displaced Owen's "Dipnoa" with "Phractamphibia." Cope, in 1868, retained essentially the same classification as proposed by Owen. In 1874 the committee of the British Association for the Advancement of Science reported on the extinct Amphibia, and placed *Archegosaurus* by itself in group VI, the Archegosauria.

No further additions were made to our knowledge of the Temnospondylia until 1875 and 1878, when Cope described *Cricotus* from the Carboniferous of Illinois and *Trimerorhachis* from the Permian of Texas. In the next year Gaudry described *Actinodon* from the Permian of France. In 1882 a decided advance was made in the separation by Professor Cope of the rhachitomous forms such as *Eryops, Actinodon, Zatrachys, Trimerorhachis* and other genera, which have subsequently proven to be synonyms of the genera mentioned, into a distinct group. Cope proposed the term Rhachitomi for this subordinal group, and designated two families, the Eryopidæ and the Trimerorhachidæ as its members. Later in the same year Cope described *Acheloma* from Texas. In 1885 Lydekker added other genera and families to the group, notably *Gondwanosaurus*, which he placed in the family Archegosauridæ. In 1884 Cope, and in the following year Fritsch, contributed further to the knowledge of the Temnospondylia by the description of the forms *Diplospondylus* and *Cricotus* from the Permian of Bohemia and Texas. In 1888 Zittel proposed to place all temnospondylus amphibians under the suborder Temnospondyli in two groups—A, those with rhachitomous vertebræ; B, those with embolomerous vertebræ—for which two groups Cope had previously, 1885, proposed the terms Rhachitomi and Embolomeri, but had regarded them as coördinate with the group Stegocephali.

Case, Broili, and others have in recent years given additional information on the forms previously described and have described some new forms. In 1909 Dr. S. W. Williston, in his essay on "*Trematops milleri* from the Permian of Texas," was enabled to give a restoration of the skeleton of that form. In the present bulletin the writer will describe an interesting new embolomerous amphibian under the name *Spondylerpeton spinatum*, from the Coal Measures of Mazon Creek, Illinois. This is the oldest of the known Temnospondylia.

We know nothing of the ancestry of the Temnospondylia. They occur in the Carboniferous and Permian, and if the Stereospondylia are highly specialized Temnospondylia, as seems probable, they also occur in the Triassic, but this is yet to be proven.

The geographical distribution of the Temnospondylia is as follows: In the Carboniferous and Permian of North America; Europe; and Asia, in the Permocarboniferous of India, *Gondwanosaurus*. So far as the writer is aware they occur nowhere else unless some of the little known forms from South Africa will, on further search, reveal temnospondylous characters. It is entirely too soon to arrive at any conclusions as to the paths of migration of this group. They followed the way which was open to other land animals, whatever that may have been.

Nor can we say in what region the first of the Temnospondylia lived. Judging from the remains so far discovered their place of origin must be located in North America. The announcement of the discovery of the eryopoid form from Pittsburg, Pa., by Case, and the discovery by the writer of the cricotoid form in the Mazon Creek fauna, as well as the presence of Carboniferous Cricotidæ in Illinois and Kansas, all point to an origin of the temnospondylous group at an earlier date in North America than in any other region of the globe. The embolomerous forms are by far the older.

The species of fossil Amphibia from the Carboniferous, Permian and Triassic are so little known that it is difficult to give a definite list of the species of the Temnospondylia. The list given below is believed to be approximately accurate. It does not differ in essential outlines from that given by Zittel in 1887. The species are distributed in the various groups to which, at the present time, they seem to belong:

CLASS—AMPHIBIA, LINNÉ, 1758.

ORDER—TEMNOSPONDYLIA, Zittel, 1887.

Suborder—RHACHITOMI, Cope, 1885.

FAMILY—ERYOPIDÆ Cope, 1882.

Eryops megacephalus Cope, 1877. Permian of Texas.
" erythrolithicus Cope, 1878. Permian of Texas.
" ferricolus Cope, 1878. Permian of Texas.
" reticulatus Cope, 1881. Permian of Texas.
" ? platypus Cope, 1877. Carboniferous of Ohio.
" latus Case, 1905. Permian of Texas.
" willistoni Moodie, 1911. Permian of Oklahoma.
Trematops milleri Williston, 1909. Permian of Texas.
Acheloma cumminsi Cope, 1882. Permian of Texas.
Ichthycanthus ohiensis Cope, 1877. Carboniferous of Ohio.
Gondwanosaurus bijoriensis Lydekker. Bijori, India.
Zatrachys apicalis Cope, 1881. Permian of Texas.
" conchigerus Cope, 1896. Permian of Texas.
" crucifer Case, 1905. Permian of Texas.
" micropthalmus Cope, 1896. Permian of Texas.
" serratus Cope, 1878. Permian of Texas.
Actinodon frossardi Gaudry, 1880. Permian of France.
" latirostris Jordan. Permian of France.
* (?) Anisodexis enchodus Cope, 1897. Carboniferous of Ohio.
* " imbrecarius Cope, 1882, Permian of Texas.
*Rhytidosteus capensis Owen, 1884. Karoo Beds, South Africa.
(?) *Euchirosaurus rochei Gaudry. Permian of France.

FAMILY—TRIMERORHACHIDÆ Cope, 1882.

Trimerorhachis bilobatus Cope, 1883. Permian of Texas.
" conangulus Cope, 1896. Permian of Texas.
" insignis Cope, 1878. Permian of Texas.
" mesops Cope, 1896. Permian of Texas.
" leptorhynchus Case, 1902. Permian of Oklahoma.
Cricotillus brachydens Case. Permian of Oklahoma.
Archegosaurus austricus Makowsky, 1876.
" decheni Goldfuss, 1847. Permian of Germany.
" latifrons Gein. & Deich. Permian of Saxony.
" ornatus Woodward, 1905. Permian of India.

Platypodosaurus ricardi Twelvetrees, 1880. Permian of Russia.
" stückenbergi Trautschold. Zechstein of Russia.
Cochleosaurus bohemicus Fritsch, 1876. Permian of Bohemia.
Gaudrya latistoma Fritsch, 1885. Permian of Bohemia.
Chelyosaurus vranyi Fritsch, 1878. Permian of Bohemia.
*Sphenosaurus sternbergi Fitzinger, 1840. Permian of Bohemia.
Sparagmites lacertinus Fritsch, 1885. Permian of Bohemia.
*Sclerocephalus hauseri Goldfuss. Permian of Germany.
*Sclerocephalus credneri Fritsch. Permian of Bohemia.
*Sclerosaurus bavaricus Branco. Rothl. Ohmbach.
*Melosaurus uralensis H. von Meyer. Kupfersandstein.
*Osteophorus roemeri H. von Meyer. Rothl. Schliessen.
*Zygosaurus lucius Eichwald. Permian of Russia.

Gonioglyptus huxleyi Lydekker from the Gondwana beds of India also possibly belongs in this family.

So many genera and species of extinct Amphibia are based on fragments of crania or limbs that an exact diagnosis of the forms is impossible. The species marked with a star (*) are uncertain as to position. Many of the species listed under the Trimerorhachidæ are placed in this family on the authority of Lydekker, who included them in his family Archegosauridæ, which was preoccupied by Trimerorhachidæ. Doctor Williston regards *Trematops milleri* Will. and *Acheloma cumminsi* Cope as representatives of a family distinct from the Eryopidæ for which in 1910 he proposed the name Trematopsidæ. He also regards the species of *Zatrachys* as entitled to family rank in the Zatrachydidæ, Williston, 1910.

Euchirosaurus of Gaudry is probably a reptile.

Suborder—EMBOLOMERI, Cope, 1881.

FAMILY—CRICOTIDÆ Cope, 1884.

Cricotus gibsoni Cope, 1877. Carboniferous of Illinois.
" crassidiscus Cope, 1884. Permian of Texas.
" heteroclitus Cope, 1875. Carboniferous of Illinois.
" hypantricus Cope, 1884. Permian of Texas.
" sp. indet. Case. Carboniferous of Illinois.
Diplospondylus punctatum Fritsch. Permian of Bohemia.
Spondylerpeton spinatum Moodie, 1910. Carboniferous of Illinois.
? *Discosaurus permianus Credner. Permian of Saxony.

FAMILY—DISSOROPHIDÆ Williston, 1910.

Dissorophus multicinctus Cope, 1895. Permian of Texas.
" mimeticus Cope, 1896. Permian of Texas.
" testudineus Cope, 1896. Permian of Texas.
Cacops aspidephorus Will. 1910. Permian of Texas.
Aspidosaurus chiton Broili, 1904. Permian of Texas.

From the foregoing diagnosis is will be seen that about 55 species of the 350 which have been assigned to the fossil Amphibia of the world can be located in the order Temnospondylia. Without doubt some of these species will prove invalid and there will be others already described which will in time prove to belong to this group, but the above statements represent an approximation of our present knowledge.

Since the present essay is to deal especially with a new member of the genus *Eryops*, only those groups will be here defined to which *Eryops* and its allies pertain.

ORDER—TEMNOSPONDYLIA, Zittel, 1887.

Terrestrial or semiaquatic vertebrata; skull bones pitted and grooved; lateral line canals present; pineal foramen sometimes absent; sclerotic plates present; vertebræ rachitomous or embolomerous; notochord usually persistent; one or two sacral vertebra; tail present, short or long; limbs and girdles all well developed; pectoral and pelvic girdles composed of the usual stegocephalan elements; an osseous pubis present; cleithrum present on the scapula in some forms; limb bones well developed and bones of forearm and leg separate; carpus and tarsus osseous, 12 elements present in tarsus of one form, 11 carpals; five digits in hand and foot; phalangeal formula 2, 3, 3, 4, 2 (?) for the hand and 2-3-3-3-2(?) for the foot; venter covered with an armature of osseous scutes, sometimes overlapping; skin of back bare or armored; ribs heavy, double-headed, curved, and either moderately long or short. Body short and heavy. As compared to skull, about two to one. Temporal foramina present in a few forms.

Range. Pennsylvanian to (Triassic) Upper Permian.

Distribution. North America—Illinois, Kansas, Oklahoma and Texas. Europe—Germany, Bohemia, France. Asia—India.

The suborder Rhachitomi is characterized solely by the nature of the vertebral column, which is cut into triangular segments.

FAMILY—ERYOPIDÆ Cope, 1882.

Large terrestrial or amphibious vertebrata; skull bones deeply marked with pits and grooves which at times take the form of lateral line canals; carpus and tarsus osseous; pubis osseous; pentadactyl fore and hind limbs; orbits in the typical genus located far back on the skull and near the median line; cleithrum present on the scapula; vertebræ rachitomous, the intercentrum supporting the arch in the dorsal region; parasphenoid well developed or reduced; teeth on pterygoids, palatines, prevomers and parasphenoid.

Range. Upper Pennsylvanian to Permian.

Distribution. America, Europe, Asia.

Genus—Eryops Cope, 1877.

The following definition of the genus is given by Doctor Branson: "Skull long, comparatively narrow; proportion of length to breadth about nine to seven. Roof bones coarsely sculptured posteriorly, finely sculptured anteriorly. Nasals and premaxillæ very large; frontals excluded from orbits by junction of pre- and post-frontals. Pterygoids not meeting in the median line; parasphenoid dagger-shaped, tapering gradually to a point just in front of the palatine foramina; prevomers large. Orbits subcircular, situated in the posterior half of the skull; nares subovate, remote, at a considerable distance from the tip of the skull. Many minute denticles on pterygoids, palatines, prevomers and parasphenoid. Teeth circular in cross section, strongly ribbed near base, dentine strongly infolded. Three large teeth on each palatine. Mandible without postcotyloid process. Vertebræ rachitomous. Ribs double-headed. Pelvic bones coalesced."

There have been up to the present five species of *Eryops* described, with a doubtful sixth, ? *Eryops platypus* Cope, from the Carboniferous of Ohio.

In 1889 Lydekker described a species of *Eryops, E. africanus,* from the Karoo beds of South Africa. Broom has subsequently shown that this species does not belong in this genus and has placed that species with two others in his genus *Rhinesuchus,* in which he includes *R. (Macromerion) gumbeli* (v. Ammon), *R. (Eryops) africanus* (Lydekker), and *R. whaitsi* Broom.

An additional species of *Eryops* is represented by remains in the collection of the University of Kansas and it is here described as new.

Eryops willistoni, new species.

Dr. S. W. Williston in 1899 described and partially figured in the *Kansas University Quarterly* portions of a skeleton of a species of *Eryops,* which he tentatively referred to the species *Eryops megacephalus* Cope. He has several times expressed to me the opinion that the form is distinct from *E. megacephalus,* and a recent careful study of the material has led me to regard the remains as a new species, which may be very appropriately named *Eryops willistoni* as a partial expression of gratitude to my honored preceptor in paleontology. Since, also, several interesting points in anatomy and morphology have come up for consideration the following discussion is presented in the hope of adding some knowledge on this peculiar Permian genus.

The material which represents the present species comprises the following portions of the skeleton: Portions of the skull; several teeth and a nearly entire right mandible; the scapula-coracoid of both sides, incomplete; the right clavicle; portion of the interclavicle; right humerus, radius, ulna and a phalange; about a dozen vertebræ and the left sacral rib.

There are various fragments of the skull preserved. On one of these fragments is observed a portion of the right orbit and a part of the prefontal and frontal bones clearly marked off by sutures. The present form differs in this respect from the known specimens of *Eryops megacephalus,* in which the sutures remained unknown until they were discovered by Doctor Branson, who was able to trace them with the aid of a lens. On the present specimen the sutures stand out with almost startling distinctness. They do not have the sharply zigzag form assumed in *E. megacephalus* and other of the larger Amphibia, but the sutures occur in bold curves. I detect a portion of the supraorbital lateral line canal on the fragment containing the orbit. The sculpture of the cranial bones in the present form is quite different from that of *E. megacephalus.* It is much more rugose and the rugosities have a larger form. This holds true for the mandible also (plate XLIX, fig. 1), and it is taken as one of the specific characters.

There are preserved in the collection also a single complete tooth and fragments of others. The complete tooth (plate XLIX, fig. 2) is of the typical labyrinthodont form. It is oval in cross section with sides flattened. It arises from a tumid base of cancellated bone as in the mosasaurs. It is recurved and sharply pointed.

In 1899 Ludwig Strickler (Paleontographica Bd. XLVI, p. 85, plates XI, XII) investigated the minute structure of the teeth of *Eryops megacephalus.*

The mandible of the present species is preserved in a much broken condition, but its form is nearly complete. The form and ornamentation of the posterior portion were well shown in

Williston's figure (Kan. Univ. Quart., Ser. A, vol. VIII, pl. XXX, fig. 1), which is reproduced here with slight changes. The sharp angulation and the posterior position of the angle is a specific character which serves to distinguish this species from *Eryops megacephalus* Cope, to which the present form is most nearly allied.

The jaw (plate XLIX, fig. 1), is heavy and elongate. The portion posterior to the coronoid angle is an acute triangle which ends in the articular. Only a portion of the suture bounding the articular can be distinguished. This is indicated in the figure. The coronoid suture is evident for its entire course. The suture starts from the articular suture, and running directly forwards turns upward just before reaching the teeth, which do not occur on the coronoid. This element is a thin bone superiorly but more thickened below. The sutures separating the angular, surangular and dentary cannot be determined. The angular and surangular contain, on their external surface, the peculiar nodose ornamentations which help to characterize the present species.

The sculpture on these elements consists of scrobiculate knobs some 5 to 7 mm. in diameter. This ornamentation ends apparently at the dentary, since the tooth-bearing element, which is quite large, is ornamented only with coarse elevations and pits.

The operculo-mandibular lateral line canal can be traced as a depression beginning on the articular and running forward as far as the bone is clearly preserved. It occurs as a shallow groove interrupted by the nodose and scrobiculate sculpturing of the mandibular elements. The internal surface of the mandible is not preserved in sufficient detail for description.

Complete teeth are lacking from the mandible in its present condition. Doctor Williston figured two of them as complete, and it is quite probable that they have been broken off since he studied the specimen, because the material is excessively fragile. The hollow character holds for all of the tooth bases which are preserved on the mandible. An additional portion of the mandible is shown in figure 5, plate XLIX. Its characters do not differ from those described above.

In regard to the hollow nature of the teeth, Tomes has the following explanation: "The laminæ of pulp, with their several systems of dentinal tubes, instead of passing out in straight lines like the spokes of a wheel, pursue a tortuous course as they run from the central small pulp chamber toward the surface. Not only do they undulate, but they give off lateral processes, and at their terminations near the surface of the tooth the thin laminæ of pulp (so thin that the radiating pulp chambers are mere fissures) become dilated; so that on section circular canals are seen at these points, as is also the case at the points where subsidiary processes branch off." (Dental Anatomy, 5th edition, 1898, p. 65.)

Measurements of the mandible of *Eryops willistoni:*

Greatest length	48 cm.
Length of posterior portion (fig. 1)	33
Greatest width	10
Width of dentary midway from coronoid process	6.5
Width across articular	2.6
Length of tooth	2.
Thickness of same at base	.5

The right arm of this species is preserved in an incomplete condition, as may be seen by reference to plate LII. The form of the humerus is well shown in the figures, plate LIII, fig. 7, and plate LII. It suggests to a certain extent the humerus of a mosasaur. The present element does not have the bizarre appearance which exists with the specimen of that element of *Eryops megacephalus* figured by Professor Cope in 1890 (Trans. Amer. Philos. Soc., vol. XVI, p. 367, fig. 3). The large projections are wanting entirely from one side and on the other they are not so highly developed, and yet the form of the bone is such that it can be nothing else save a humerus. It is too rugged for a femur.

The specimen is abraded to some extent, so that the exact form of the element cannot be determined. It may have had the form suggested by the broken lines in the figures. The humerus is that of the right side. Viewed from in front the element is seen to have a peculiar form (plate LIII, fig. 7). The lower portion of the inner surface is distinctly concave. The inner side of the bone is comparatively smooth. There is a low ridge which runs obliquely across the antero-superior angle of the bone. There is a distinct twist in the inner surface, which is continued to such an extent that the inner surface is carried around almost parallel with a portion of the outer surface. It then takes another and inward curve and ends in a projection.

One of the projections from the outer surface of the humerus is in the form of a hook and strongly suggests the hooklike process which is developed in the quadrate of the mosasaurs. This hook and the other elevations on the edge of the bone without doubt served as points of attachment of the deltoid and pectoralis muscles, which were undoubtedly well developed in the species of *Eryops*.

The outer surface of the bone is exceedingly rough and there are no less than six distinct elevations on this surface. One of these elevations is a ridge which runs at somewhat of an angle across the posterior edge. There is an indication of a foramen opposite the pit which occurs on one side of the bone, which at first was thought to represent the entepicondylar foramen. This was such an important matter that the bone was cut through at this point by Mr. Martin and fully demonstrated the total absence of this foramen in the element although there is quite a distinct pit at this point. Cope described such a foramen in *Acheloma*, but Case, who has recently examined the type, says the foramen is an accidental opening. Gaudry likewise described such an opening in *Actinodon*.

Measurements of the humerus:

Length of specimen as preserved	96 mm.
Estimated length along same line	110
Width at middle of shaft	50
Width of top of humerus	90
Width at lower end	72
Thickness of head as preserved	23
Diameter of entepicondylar pit	3

The element which is here regarded as a radius is very similar in form to that described by Cope for *Eryops megacephalus*. Its form is well shown in the figure. The lower end is somewhat larger than the upper, which is abraded and broken. Viewed from the lower surface a cross section of the bone shows a semicircular form. It is hour-glass shaped in its entire length, with a shallow groove near the lower end. Both ends of the bone near the articular surfaces are roughened by vascular pits for muscular attachment or for the union of the cartilaginous tips.

Measurement of radius:

Actual length of specimen	91 mm.
Estimated length of specimen	95
Width of upper end (estimated)	40
Width at middle of shaft	24
Width at lower end	60
Thickness of base	32

The element here figured as an ulna (plate LII, *U*) is doubtfully referred to the arm, since the bones were found disassociated. It may belong to the leg. Its form is specifically different from that which Cope figured as the ulna of *Eryops megacephalus,* although its form is, in general, the same. It does not depart widely, in point of form, from that of the radius, which we should expect to be the case in a generalized vertebrate. It is smaller, somewhat shorter, and the groove on the ventral (?) surface is lacking. The radius and ulna are both peculiarly amphibian in the way they have weathered. The ends have assumed the concave form so characteristic of the Branchiosauria and the modern Amphibia, indicating a higher development of the perichondrium than of the endochondrium.

Measurements of the ulna:

Actual length of specimen	80 mm.
Estimated length of specimen	93
Width of shaft at middle	22
Width of upper end (estimated)	47
Width of lower end (estimated)	40

Associated with the limb bones there is a portion of a phalange of the hand (?) of the specimen. There are no carpals preserved. The element figured (plate LIII, figs. 4 and 5) is probably a metacarpal. Its form is very closely similar to that figured by Cope for the metacarpal element of *Eryops megacephalus.* Its upper end is very broad, with recurving edges and with rugosities for muscular attachment. Its form is crescent shaped and concave. The shaft narrows abruptly from the upper end to the middle and then widens for the lower end, which is lost.

Measurements of the metacarpal:

Actual length of specimen	23 mm.
Estimated length of bone	27
Width of upper end	22
Thickness of upper end	8

The following description of the coraco-scapula (plates L, LI) is taken from Doctor Williston's paper. The description of the cleithrum is appended:

"The bone is elongated, and nowhere very thick or massive. The distal part of the scapula is much thinned and considerably expanded; the immediate margin here, however, is wanting, so that the precise outlines cannot be given.

"The position of the two bones must have been very oblique, as is evident from the position of the glenoid cavity. The postero-inferior border is moderately thickened, and rounded; gently concave along the proximal part and convex distally. The antero-superior border is much thinner than the opposite one, and is concave throughout the extent of the shaft, except distally, where it is coössified with the procoracoid. The union of these two bones is very close in this region, the sutural line being distinguished with difficulty if at all. The procoracoid is narrower and more thickened below, reaching to the lower part of the conjoined bone, and lying in close apposition though not suturally united. Both the lateral surfaces of the scapula are nearly flat. A little proximad to the narrowest part of the shaft the bone is much thickened by a stout ridge on the inner side, which includes between it and the remainder of the bone, just back of or above the cotylus, a large, elongated foramen, both of whose orifices can be seen from the inner side of the bone only.

"The glenoid surface is elongated and deeply concave in its long diameter. The scapular portion is much smaller than the coracoid, and is partly separated from it by a constriction; this surface is nearly flat and is placed at right angles to the plane of the coracoid surface, looking directly downward when the bone is lying horizontally. The rest of the cotylus is moderately concave and looks outward and somewhat backward and upward with the bone in its former position. Just how much of the conjoined bone is formed of each element it is impossible to say since the union is so close that no trace of a junction is perceptible. Evidently, however, the coracoid forms only a small part of the whole bone. Its anterior or inferior border is gently convex, the posterior one slightly concave.

"The anterior end of the superior border of the scapula is gently convex, as is also the broad external surface. On the inner side the foramen described above opens into a deep, elongated, boat-shaped cavity at its distal end, the cavity formed by the upper border of the ridge described. In the lower or anterior end of the cavity there are apparently two smaller foramina, the external orifices of which are just within the anterior margin of the scapular face of the glenoid surface. The proximal surface of the scapula is concave; that of the coracoid, if the bone is limited by the ridge spoken of, is for the most part gently convex and lies in a more mesial plane."

The scapula is evidently that of the right side, the same as the humerus described below.

On the antero-superior corner of the scapula is a part of a peculiar element—the cleithrum. Its occurrence in the genus *Eryops* has been noted by Case in two species. In *E. latus* the cleithrum takes a most peculiar form. The form assumed by the element in the present species is impossible to determine, since the greater part of it has weathered away.

The cleithrum is, apparently, simply laid on the upper edge of the scapula, the union being hardly a sutural one. In the present specimen it is represented only by the lower part, but it could not have had the immense expanse superiorly as Case and Williston have figured for the cleithrum in *Eryops latus* Case. It was probably quite slender, as it is in the dicynodont reptiles. The cleithrum is a thin plate of bone with a ridge running along the interior border. The edge of the scapula is depressed to receive the element.

The characters of the scapula which are at variance with the scapulæ of the known species are the narrowness of the shaft, the location and size of the cleithrum, and the position of the cotylus.

In regard to the three foramina seen and described in the scapula Williston has recently proposed the terms supra-, post- and infra-glenoid or supra-coracoid to designate these openings. The foramina occur in all known Temnospondylia, as well as in the Cotylosauria (2) and in the Pelycosauria (2). The writer has recently described a branchiosaurian from the Pennsylvanian of Mazon Creek in which three foramina are visible in the scapula. This was thought to be of interest in connection with the Temnospondylia, but investigation showed that in the temnospondyles the foramina are in no case to be regarded as occurring strictly in the scapula, but rather as belonging to the coracoid which is united with the scapula.

An interesting question of homologies, or it may be parallel development, arises in comparing the present scapula-coracoid with the clavicular apparatus of *Portheus*.

Measurements of scapula-coracoid:

Actual length of specimen	33.7	cm.
Estimated length of element	36	
Width of upper end of scapula	15.5	
Thickness at upper end	3	mm.
Width at middle of shaft	6.6	cm.
Width across coracoid portion	17	

Length of cotylus	7.2	
Width of cotylus	3.8	
Diameter of infraglenoid foramen	5	mm.
Thickness of bone at lower edge	7	
Thickness of bone through cotylus	4.3	cm.
Length of portion of cleithrum preserved	63	mm.
Greatest width of cleithrum	22	

The clavicle of the right side is preserved almost completely (plate LIII, figs. 1 and 2). The element was figured by Doctor Williston but not described. It is strongly curved and spatulate. Its outer surface is ornamented with longitudinal grooves, which arise near the center of the bone and run each way, thus indicating its ossific center. The inner surface of the bone is smooth excepting for two vascular pits near the center. A prominent ridge runs along the dorsal inner edge of the bone.

Measurements of the clavicle:

Length along curve	24.7	cm.
Length across arc	20	
Least width	1.3	
Greatest width	4.6	
Greatest thickness	1	
Least thickness	2	mm.

There is a fragment of what I regard as the posterior projection of the interclavicle. If it is such it is either a pathological specimen or there were two projections from the posterior edge of the interclavicle, for the fragment is highly asymmetric. The spine, for such it is, has an irregular nodose surface as if for the attachment of cartilage. It is long, slender and somewhat flattened. (Plate LIII, fig. 3.)

Measurements of spine of interclavicle:

Length of specimen	13.7	cm.
Greatest width	2.2	
Least width	.75	

There are remains of about a dozen vertebræ preserved. Portions of three of these are figured in plate LIV, figures 1 and 2. They all have the characteristic rachitomous form assumed by the other species of *Eryops*. The divisions between the pleurocentra, hypocentra and neurocentra are well marked. The zygapophyses are well formed. The upper part of the neural spines is much thickened, as is the case often in specimens of *Eryops megacephalus* Cope. According to Broili the spines may also be bifurcate, as Cope has described for *E. erythrolithicus*. The enlarged spine was undoubtedly for the attachment of muscles to sustain the enormous head, and spines showing different characters might very easily occur in various portions of the vertebral column.

Measurements of vertebræ:

Length of centrum	2.5 cm.
Width of centrum	3.2
Height of vertebræ to tip of spine	13.4
Thickness of top of spine	3

Broili (Monatsb. d. Deutsch, Geol. Gesell., Bd. 60, Texttafel p. 236, fig. 2) has figured in *Eryops megacephalus* a peculiar element which he has identified as the sacral rib, having found it in place with a sacral vertebra. There is no doubt that the present element (plate LIV, figs. 3 and 4) is the same as he has figured. Its interpretation as a sacral rib is somewhat surprising on account of the extreme thinness of the bone. It thins out to less than a millimeter on one edge. Its location any other place in the skeleton is, however, doubtful.

The element has a broad base as if for attachment suturally with the vertebral transverse process. The base of the specimen has been broken transversely and only a portion of the suture remains. The bone is flat immediately from the base and is greatly expanded and thinned distally. It is, for the most part, smooth, though there is a small roughened place on the dorsal (?) surface. The ventral (?) surface is marked by a depression which runs the entire length of the bone. The distal end is lost.

Measurements of sacral rib:

Actual length of specimen	90 mm.
Width at distal end	62
Width at middle of blade	32
Width at inner end	55

Eryops willistoni differs from *E. ferricolus* Cope in the absence of a raised rim to the orbits. From *E. erythrolithicus* Cope it differs in the non-bifurcation of the neural spines. This last is not a well-known species and may be synonymous with *E. megacephalus*. *E. reticulatus* is a small species, from which *E. willistoni* differs in the character of the cranial sculpture. It is distinct from *E. latus* Case on account of the dimensions of the scapula and the cleithrum. *E. megacephalus* also shows characters which are divergent from those of the present species. These are the shape and structure of the mandible and its ornamentation, the form of the humerus and the shape and structure of the scapula-coracoid, as well as other structures which are characteristic.

The material on which the species *Eryops willistoni* is based is from the Permian of Oklahoma. It was collected by Prof. C. N. Gould in 1896, in the red sandstone southwest of Blackwell, Okla. The specimen is No. 348 of the Kansas University Museum.

I am indebted to Mr. G. Dallas Hanna for all of the drawings illustrating the present essay, except that on plate XLIX figure 1, which is from the pen of Mr. Sydney Prentice, at present with the Carnegie Museum.

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CONTENTS:

An Armored Dinosaur from the Upper Cretaceous of Wyoming,
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AN ARMORED DINOSAUR FROM THE CRETACEOUS OF WYOMING.

BY ROY L. MOODIE.

(Contribution from the Zoölogical Laboratory, No. 190.)

Plates LV to LIX, and one text figure.

IN *Science* for October 20, 1905, Dr. S. W. Williston (*1*) published a brief account of a remarkable armored dinosaur from the upper Cretaceous of Wyoming. He likewise gave a short sketch of the horizon from which the specimen was obtained, naming the horizon Hailey shales, and suggesting the name *Stegopelta landerensis* for the dinosaur.

During the summer of 1906, while searching these beds for plesiosaur remains for the Carnegie Museum (*2*) the writer followed the horizon eastward and northward to the southern end of the Big Horn mountains. The beds increase in thickness towards the east and the lithological character becomes different, changing from a soft fine shale in the west to a hard sandy rock in the Big Horn region. The Hailey shales lie just above and comformable on the Mowry beds, which Darton (*3*) describes as follows:

"The stratigraphic succession of the formation [Colorado] is uniform throughout. The lowest beds are several hundred feet of dark-colored shale, usually containing toward the base a deposit of sandstone from 2 to 20 feet thick. This is capped by the Mowry beds, consisting of from 100 to 150 feet of hard shales and thin-bedded, fine-grained sandstone of a dark gray color, which on exposure weathers to a characteristic light gray. These rocks are especially characterized by large numbers of fish scales in nearly every bed. They are often so abundant as to number from five to ten on a surface of six inches square. Owing to their hardness the beds give rise to round-topped ridges of considerable prominence."

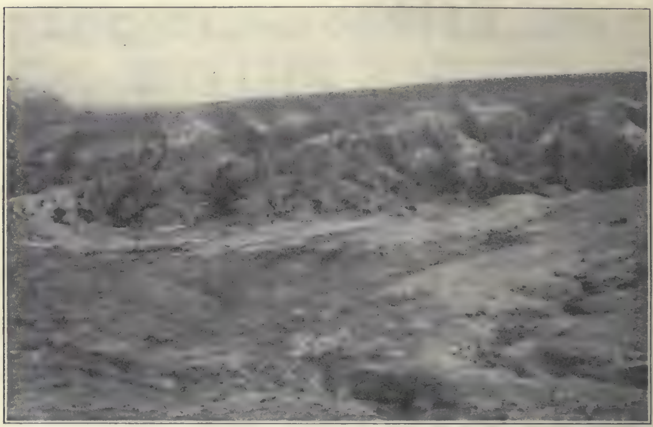

FIG. 1. A typical exposure of the Hailey shales on Connant creek, Wyoming. The Mowry beds may be seen on the left in the background.

In those parts of Wyoming where I worked, the Mowry beds stand out as prominent ridges of hard whitish shales which can be readily recognized from a long distance, and on that account serve as excellent landmarks for the identification of a region where the Hailey shales may occur. In thickness the Hailey shales vary from a few feet north of Lander, Wyo., to something over 200 feet in the Big Horn region. "Near Soap Creek the dark shales overlying the Mowry beds are about 200 feet thick," etc. (*6*). In most of their extent the Hailey beds have numerous brown sandy clay concretions which very often contain vertebrate remains. These concretions vary in size from a few inches to many feet in diameter. In the Big Horn region the concretions are stratified into distinct layers, but such is not the case in other places where the horizon was examined.

So far as is at present known the Hailey shales outcrop along the eastern flank of the Wind River mountains, in the Shoshone anticline; in the anticline along Beaver creek near Hailey, Wyo., the type locality; in an anticline north and west of the

Granite mountains, on Connant creek; in a small anticline west of the Rattlesnake mountains; along the northern and eastern flanks of the Rattlesnake mountains. There are extensive exposures on the eastern slope of the Big Horns, and I do not doubt that they occur also to the west of these mountains. In text-figure 1 is given a view of a typical exposure of the Hailey shales, on Connant creek, north of the Granite mountains, Wyoming. On the left of the photograph the Mowry beds stand out in the characteristic ridge.

The vertebrate fauna of the Hailey shales still remains to be accurately determined, but so far as known it is represented by large and small fishes, amphicœlian crocodiles with hollow limb bones, turtles with completely ossified carapaces and plastra like *Toxochelys* and plesiosaurs of two types. The remains of plesiosaurs are in places exceedingly abundant, evidences of no less than fifty-five individuals having been discovered during one summer. Occurring in these deposits, also, have been discovered the remains of three dinosaurs. The remains described below represent one of these animals. The other two are known in one case from a single worn dorsal vertebra found in one of the massive shell-concretions consisting of myriads of gastropod and lamellibranch shells together with plesiosaur teeth and vertebræ, about ten miles north of where the *Stegopelta* remains were exhumed; and in the other case from three caudal vertebræ discovered in the same beds nearly a hundred miles to the east, near the western base of the Rattlesnake mountains.

The *Stegopelta* remains herein described were once encased in one of the brown sandy clay concretions so abundant in this formation, but many years ago it was exposed and by the weathering processes of a long space of time had become reduced to hundreds of fragments. These fragments had washed and rolled down the slope and had been trodden in the mud by cattle so that when first discovered it was discarded as a worthless plesiosaur specimen. When Doctor Williston, however, in cleaning up some of the fragments came across some typical stegosaurian dinosaur teeth, the whole aspect of the matter was changed and every fragment was carefully collected. As boxed the specimen weighed only 450 pounds, of which about two-thirds was bone. It has been a long and tedious task to fit together the scattered and disassociated fragments, but through the combined efforts of Doctor Williston and myself a number of elements of the skeleton have been reconstructed.

The specimen as it now stands consists of the following parts: Fragments of the upper and lower jaws with a dozen or more teeth, most of which are fragmentary; seven fragmentary dorsal vertebræ; portions of the sacrum; two caudal vertebræ; many fragments of the ribs; a complete ulna belonging to the left side; portions of the right ulna; portions of the radii; the left ilium nearly entire; a part of the right ilium, showing the acetabulum; the right pubis nearly entire; a portion of the left pubis; the lower portion of the right tibia; the upper and lower ends of the right fibula; many large fragments of the metatarsals; nearly a hundred small bony scutes; several large bony plates, girdles and bony spines representing various portions of the dermal armor; together with a great quantity of waterworn fragments which it is impossible to determine.

The remains described as *Stegopelta landerensis* indicate a stegosaurian dinosaur about two-thirds the size of *Stegosaurus ungulatus* Marsh. The head was small, as is indicated by the size of the teeth. The fore limbs were not relatively so large as in *Stegosaurus.* The entire pelvic region was covered with a dorsal shield of rather thick, scrobiculate plates with elevated centers which are asuturally united over the pelvis. On each plate there is found, either on one side or in the central eminence, a pit, which possibly supported a more or less elongate horny spine. Anterior to the pelvic shield there were many dermal plates and scutes of various sizes scattered over the dorsal region of the body. The anterior portion of the animal appears not to have been armed. Back of the pelvis there were massive dermal plates, huge bony spines and a bony girdle probably encircling the tail in some such manner as in the glyptodonts. The neural spines of the caudal vertebræ were probably each surmounted by an elongate bony plate which quite possibly bore a horny excrescence of some kind. While closely similar in many respects to *Polacanthus, Stegopelta* shows wide structural differences from that form, although it must have had much the same appearance as Nopsca (*5*) has figured in *Polacanthus.* The present dinosaur, in life, may have stood nearly seven feet high at the hips and attained a length of sixteen to eighteen feet. Armed as it was with horns, spines and excrescences it must have been a bizarre creature, even in those Cretaceous days.

The teeth (plate LVI, figs. 4 and 5) of *Stegopelta* are typically stegosaurian. There are a dozen of them in more or less perfect state of preservation. They are all of practically the same size and character, showing but little variation among themselves. The crowns of the teeth, which measure 7 mm. in breadth, are subcompressed and narrowly palmate with eight radiating costæ, all of which end at the tip in sharp points. The roots of the teeth measure 15 mm. from the base of the crown to the tip of the fang. In point of size and number of costæ the present teeth are so closely similar to those described by Leidy (*5*) as a supposed lacertilian form, *Paleoscincus*, that had the teeth only been found they would undoubtedly have been referred to that genus. It is possible that *Stegopelta* may eventually prove to be a *Paleoscincus* form. This, however, is hardly probable, on account of the great interval of time separating the strata which have yielded the two specimens, *Paleoscincus* occurring as it does near the top of the Fort Pierre Cretaceous and *Stegopelta* near the top of the Fort Benton. Were the form one of a stable group this might not be sound reasoning, but in a group of animals which evolved so rapidly as did the dinosaurs one would hardly expect a genus to continue for so long a time. At all events, the name *Stegopelta* may be retained until more evidence is forthcoming concerning *Paleoscincus*. If, as Hatcher believed (*23*), Lambe's *Stereocephalus* is a *Paleoscincus* form, then *Stegopelta* is a good genus, since it shows wide structural differences from the form which Lambe has described. The tooth which Lambe (*7*) has figured on page 57 certainly resembles those of *Paleoscincus*, and if the tooth really is to be associated with the remains described as *Stereocephalus* a question might arise as to whether these remains were not in reality portions of the skeleton of *Paleoscincus* as Hatcher intimated. Lambe (*8*) says the tooth provisionally associated with the *Stereocephalus* remains "differs from those of the Red Deer river district, referred to the two species of *Paleoscincus*, and is about twice as large as those of *P. costatus*." Just how it differs he does not say, and one is at a loss in attempting to separate the forms from his figures. Size alone is usually no safe criterion for the separation of animal forms, and more particularly genera. I can but agree with Hatcher that the tooth figured as *Stereocephalus* resembles the teeth of *Paleoscincus.*

The *vertebral column* is represented by posterior dorsal vertebræ, portions of the sacrum and two caudal vertebræ. The remains are more or less fragmentary, but enough is preserved to give a fairly accurate idea of this portion of the animal's anatomy, although it is impossible to determine the vertebral formula.

The *dorsal vertebræ* (plate LVIII, figs. 5 and 6) obtained are twelve in number, for the most part imperfectly preserved. They are cylindroid in form, very slightly amphicœlous, nearly amphiplatyan, and the arches are elevated as in *Stegosaurus* and *Polacanthus.* The centra are slightly excavated below the base of the neural arch as in *Scelidosaurus.* The neural canal is small and is wider in the ventral than in the dorsal portion. The centra measure 60 mm. in width by 70 mm. in length.

The *sacrum* (plate LIX, figs. 6 and 7) as preserved consists of two sections. One includes three firmly coössified vertebræ of the posterior end and the other a part of the anterior end representing two vertebræ. The anterior section measures 120 mm. in length by 70 mm. in width at the widest part. The fragment is very smooth and of a dense bony texture. The neural canal is broad posteriorly but narrows somewhat anteriorly. In plate LIX, figure 2, is represented a cross section through this fragment to show the sacral enlargement at the posterior end. The portion representing the posterior end of the sacrum (plate LIX, figure 7) measures 203 mm. in length by 64 mm. in width at the caudal end. The texture of this part is very fine and compact externally, but internally there is a tendency to a cancellated structure. An interesting characteristic of this element of the skeleton is the high degree of coössification of the various elements composing it. There is not the slightest indication of a suture where the different vertebræ have become joined so that the sacral centra are constituted in a solid bony rod tapering somewhat at the anterior end, as do the sacra of *Polacanthus* (*9*) and *Hylæosaurus* (*10*). The attachments for the sacral ribs are large, and are placed about midway dorso-ventrally of the centra of the sacrum. While the sacrum of *Stegopelta* resembles in a great measure that of *Polacanthus,* yet it varies from it in that the elements composing it are more highly coössified. This condition cannot be entirely attributed to the age of the individual but is expressive rather of the higher specialization of the present form.

Attached to the neural spines of the sacral elements was a long, narrow dermal plate (plate LVI, fig. 3), evidently in firm union with them. This plate occupied the mid-dorsal line of the great pelvic shield and lay between the iliac armor of the two sides. The plate, like all the rest of the dermal skeleton, is scrobiculate and somewhat of the texture of woven cloth, as Marsh has described in *Nodosaurus textilis* (*11*). It becomes slightly expanded posteriorly, where it measures 30 mm. in width.

The *caudal vertebræ* (plate LIX, fig. 1, and plate LVIII, fig. 3) vary to a remarkable degree from those of the dorsal series. They are greatly compressed dorso-ventrally; are very short, with the sides much rounded and the centra plano-convex. The vertebræ have strong transverse processes. In neither specimen is the neural spine preserved, so it is impossible to say as to its extent. This, however, may be inferred to have been low and stout, if one may judge from its broken bases. The neural canal is not large, measuring only 14 mm. in diameter. The centra measure 82 mm. in width by 38 mm. in length by 41 mm. in height. It is thus seen that the caudal vertebræ are more than twice as wide as long. This condition is not a unique one, since Hulke (*12*) has described the same condition in *Polacanthus.*

The *ribs* are all so fragmentary that no discussion of them can be given. Many of the fragments are triangular in cross section, agreeing in this respect with other armored dinosaurs. Attached to some of the rib fragments are found small bony scutes. The fact is of service in determining the position of these dermal scutes on the body of the animal.

The *ulna* (plate LIX, figs. 8 and 9) of the left side is preserved complete. It shows considerable variation from anything hitherto described for any other armored dinosaur. The shaft of the bone is flattened from side to side and is twisted from right to left. It ends in a rather pronounced expansion distally. The coronoid process is quite prominent and is excavated to form a large sigmoid cavity. The olecranon is long, measuring 70 mm. in length from the base of the coronoid process to the proximal end of the bone. It is flattened from side to side and ends rather broadly, not in a point as does the ulna of *Stegosaurus*. Viewed from in front the ulna curves strongly outward, especially toward the distal end. It is not so straight as in *Stegosaurus*. The articular surface for the humerus is small. The radial articulations are, however, well marked, with the upper one forming a distinct fossa below the coronoid process. The lower articular surface of the ulna is well rounded and is oval in outline. The ulna measures 385 mm. in total length, 106 mm. antero-posteriorly at the widest part, 45 mm. near the middle of the bone and 60 mm. at the proximal end.

The *radius* is represented by fragments only. The head of one of the elements is nearly circular in outline and measures 60 mm. in cross section. The articular surface is so abraded that it is impossible to determine its form.

The *ilia* (plate LV) are both represented in the collection. The left one is preserved nearly entire. Enough is present to determine the total length and breadth of the bone, and the missing parts have been restored, as is evident from the photograph. The portion of the right ilium preserved shows the acetabulum. The description of the ilium will, however, be confined to that of the left side. The bone is elongate and slightly convex upwards; the convexity becoming strongly pronounced on the outer side. It is 50 mm. thick at the acetabulum, but thins to 5 mm. on the inner side and at the anterior end. The thinning is gradual in these two directions. On the outer edge, however, the bone remains thick for over three-fourths of its length, when it gradually thins, but not so much as on the inner edge. The entire dorsal surface of the ilium is covered by a mosaic of thick, bony, scrobiculate plates firmly united to it. These plates are more or less pentagonal in shape and are not all of the same size. On nearly all there occurs, on some in the center, on others near the edge of the plate, a pit, which in life may have supported a more or less elongate horny spine. When the pit is central it is located in the top of the central eminence which occurs on all of the plates. The plates were once, apparently, suturally connected, but there is now no indication of a suture. They form one continuous bony mass over the entire dorsal surface of the ilium. The diameter of the individual plates varies from 56 mm. to 105 mm., and they are all from 5 mm. to 15 mm. in thickness. A single plate is shown natural size in plate LVI, figure 8.

The lower surface of the ilium is nearly smooth. The only irregularities are the acetabulum and small ridges for muscular attachments. It is gently concave, the concavity becoming stronger towards the outer edge. The acetabulum is in the shape of an elongate oval and is defined by a high ridge of bone. The acetabular cavity is rather shallow and is deeper anteriorly than posteriorly. Its length is 190 mm. and the width, as preserved, is 82 mm. It may have had a somewhat greater width, but not to exceed 90 mm. at the most. The entire ilium measures 48½ inches in total length, 10½ inches at the widest part, and 8½ inches near the middle of the bone.

The ilium must have had a horizontal position during life, for the position of the acetabulum is such that the femur could not have articulated in it had the bone been in any other position. This condition is not exceptional among dinosaurs, since the ilia of *Polacanthus* had a similar position and the ilia of *Triceratops* are horizontal to a much less extent. The articular surfaces for the pubes and ischia have been broken away and lost, so it is impossible to determine the relations of these elements. However, they must have had much the same relations as Seeley (*13*), Lydekker (*17*) and Hulke (*14*) have described for *Polacanthus*.

The *pubes* (plate LVIII, figures 1 and 2) are both represented, the right one nearly complete but lacking the entire post-pubic process. This element resembles more nearly that of *Claosaurus* (*15*) than it does that of its nearest allies, *Polacanthus* (*13*) and *Stegosaurus* (*16*). In form the bone is elongate, flattened and spatulate. It curves gently inwards and is only slightly twisted. In thickness the pubis is nearly uniform, becoming thickened proximally to support the pectineal process (ectopubis of Baur). The pubis measures 300 mm. exclusive of the pectineal process, which is 57 mm. in length. In width the bone measures 112 mm. at the widest part and 86 mm. at the distal end. The external surface of the pubis is crossed by a diagonal ridge for muscular attachments. The post-pubis is not represented in the collection save by a fragment which may represent the disal end. The place where the process has been broken from the pubis is large, so the post-pubis may have been of some extent.

The *tibia* (plate LVIII, figure 4) is represented by the lower end of the bone belonging to the right side. Firmly coössified with it is the astragalus, which rises into a rather prominent ascending process on the anterior surface. The union of the astragalus with the tibia is so complete that were one to view the specimen from the posterior side its presence would never be suspected. On turning the bone over, however, the astragalus is distinctly seen, as is shown in the figure. The spine of the astragalus is broken off, but judging from the groove for its reception it must have been nearly 80 mm. in length. It measures 50 mm. in width at the base. The tibia measures 145 mm. in width distally. The articular surface is broad and pulley-shaped. There is a broad, shallow, trochlear groove which is bounded by two rounded projections. The groove runs up prominently on the posterior surface of the bone but is not so prominent on the anterior surface. From the narrowness of the broken surface of the bone, only 50 mm. in diameter, one would judge that the shaft of the tibia was very slender as described by Hulke (*18*) in *Hylæosaurus* and in *Polacanthus* (*19*). It resembles these forms also in that the shaft of the tibia is triangular in cross section, forming in this case a nearly isosceles triangle. The section shows a marked difference between the exterior of the bone, which is smooth and compact, and the interior, which is coarsely cancellated.

The *fibula* (plate LIX, figures 4 and 5) is represented by the proximal and distal portions of the bone belonging to the right side. The proximal end, which is subtriangular in cross section, measures 85 mm. in width and is considerably expanded as compared to the shaft. The upper end is so weathered that no traces of the rugose surface for the attachment to the tibia are left. However, one side is flattened as if for such a union. The external side of the head is marked by a rather prominent condyle, which projects some 5 mm. from the surface. The shaft of the bone is very slender. At a distance of five inches from its upper end the fibula measures 20 mm. by 30 mm. in diameter being thicker antero-posteriorly than from side to side. In structure the fibula is much like that of the tibia, already described. The distal end, also, triangular in cross section, is of the same proportions as the proximal end.

The *metatarsals* (plate LVIII, figure 7) are represented by several fragments. The proximal and distal ends of one of them are preserved so that a reconstruction is possible. These fragments represent a rather elongate, slender element with the upper surface rounded and the lower surface somewhat flattened. The proximal articular surface is widely concave and the distal end is pulley-shaped. It is thus evident that the metatarsal is not different from that of other herbivorous dinosaurs. The length of the bone as restored is 150 mm., the breadth of the proximal end is 80 mm., and the height 60 mm.

The *dermal armor* consists of small bony scutes, large dermal spines and heavy plates, all of various shapes and sizes. Mingled in with the other bones of the skeleton were more than four score small bony scutes (plate LVII), varying in diameter from 15 to 75 mm. and of various thicknesses from 4 to 20 mm. The scutes are all scrobiculate and are for the most part rounded, though some are elongated, one scute before me measuring 60 mm. in length by 30 mm. in breadth. The majority of them possess a ridge asymmetrically placed, which runs nearly the entire length of the scute. Others run up to a point in the center; others are flat.

In structure all of the scutes are of a coarsely cancellated character, such as Hulke has described for the scutes occurring in *Polacanthus*. Associated with them were many fragments of heavy triangular ribs with which some of the scutes were firmly united. From this fact it would appear probable that the scutes were scattered along the back of the animal anterior to the great pelvic shield. The elongated scutes referred to above may possibly have been situated on the neural spines of the vertebræ, as in *Scelidosaurus* (*20*). The larger scutes, some of which are as large as the palm of one's hand, were very probably located near and anterior to the great pelvic shield.

Scutes very similar to these described for *Stegopelta* are found in a number of different armored dinosaurs as well as among the crocodiles. There are really no structural differences between the scutes of *Stegopelta* herein described and those found in the common Mississippi alligators. The pittings on the *Stegopelta* scutes are, however, smaller than in the latter. Hulke (*21*) has described a few scutes belonging to *Polacanthus* which resemble the present specimens very much. Lambe (*22*) has figured three scutes associated with the form *Stereo-*

cephalus which are almost identical with the scutes of *Stegopelta.* Hatcher (*23*) was certainly in error in criticizing Lambe's association of these scutes with dinosaurian remains and in claiming that they were of a crocodilian nature, since in the present specimen there can be no doubt as to their dinosaurian character. Nopsca (*24*) has also fallen into the same error as did Hatcher when he says that crocodilian remains were associated with the *Polacanthus* specimen. Seeley (*25*) has described and figured scutes similar to the above in *Crateomus.* Huxley (*26*) has described and figured identical scutes in *Acanthopholis.* Marsh (*27*) has figured some small bony scutes in *Triceratops.* Owen has figured scutes of a like nature in *Scelidosaurus* (*20*). Possibly other armored dinosaurs possessed such scutes.

The question of the morphological value of these scutes is an interesting one. Judging from the scutes in *Stegopelta,* one would incline to the opinion that they represent the rudiments of a complete bony armor which in time, had the dinosaurs survived, might have covered the whole dorsum of *Stegopelta's* descendants. Such a suggestion might apply equally well to our modern crocodiles. It is pretty certain that the scutes in the crocodiles are not vestigial, since it is not now conceded that the modern Crocodilia are descended from the ancient armored teleosaurs (*28*).

The *dermal spines* (plate LVI, fig. 1, plate LIX, fig. 3) are all of a dense bony texture with the external surface pitted. A portion of a small dermal spine is represented, natural size, in plate LIX, fig. 3. Its base is broken away so it is impossible to determine its extent, but this was, in all probability, not considerable. One of the most peculiar portions of the dermal armor is that represented in plate LVI, fig. 1, which is called a large dermal spine, and which I have provisionally located near the base of the tail. The spine is asymmetrical and is lateral in position, having had a mate on the opposite side of which nothing remains.

The spine preserved is much broken and the distal tip is lost. As reconstructed it is of massive proportions in comparison to the rest of the exoskeleton. In cross section it is for the most part triangular, with two sides of the triangle concave and one convex. It is rounded near the distal end. The spine, unlike most elements of a similar nature, is bifid, as is represented in the figure (plate LVI, fig. 1). The short spine measures 80 mm. from the point of its inception to the tip, and the main spine measures 16 inches from tip to tip. At its widest part it is 100 mm. in breadth. The surface of the bone is pitted with irregularly placed cavities as though it were encased with horny substance.

The exact position of this large spine on the body of the animal is, of course, largely a matter of conjecture, since it was found broken and disassociated and mingled with various other parts of the skeleton, but it seems best to locate it back of the pelvic shield, since the caudal vertebræ are much stouter than the dorsal ones and since there is no evidence of any armor excepting the small bony scutes anterior to the pelvis. The spine is totally unlike anything described for any other stegosaurian dinosaur.

The *dermal plates*, represented in plate LVI, figs. 2 and 9, are massive and of a compact texture. Their position on the skeleton is a puzzle. The plate represented in plate LVI, fig. 9, is not entire. It is asymmetrical, one side being crossed by a rather high ridge. Its upper surface has pittings and grooves. The under surface is smooth and rounded. It is possible that this is a portion of another girdle similar to the one described below. That it is not a part of that girdle is evident from its proportions. The plate measures 105 mm. in diameter. The other dermal plate (plate LVI, fig. 2) is apparently complete, with a broad surface for articulation with some element which is now lost. This plate is concavo-convex. It measures 140 mm. across in the longest diameter. It is without vascular markings of any kind, but is smooth as though it were entirely embedded in the flesh of the animal.

The part of the *girdle* represented in plate LVI, figs. 6 and 7, is like the last described plate in that it is of a compact texture. In the girdle the upper surface is pitted, and crossed at regular intervals by rather high ridges the sides of which are slightly concave. This bone at once reminds one of the similar element figured and described by Lambe (*29*) as occurring in the *Stereocephalus* form. Lambe (*29*) however, located the girdle back of the head, and if his interpretation of the large fragment which he calls the skull is correct such a location would be quite plausible. The present girdle differs in a great degree from that described by Lambe, since it is asymmetrical and had a mate on the opposite side, of which there are fragments in the collection. It differs further in being a solid mass of bone instead of a bony ring to which the scutes are united. The girdle as preserved is in the form of an arch and is composed of three plates, only two of which are ridged. The under surface is smooth and longitudinally convex. The part of the girdle preserved measures 320 mm. in length and 110 mm. in width.

Stegopelta finds its nearest allies in *Polacanthus,* from the Wealden of the Isle of Wight; in *Paleoscincus,* which must, I think, include the *Stereocephalus* of Lambe, from the Belly river deposits; and *Stegosaurus,* from the Lower Cretaceous of Wyoming and Colorado. The characters which separate *Stegopelta* from *Stegosaurus* and *Paleoscincus* have already been considered. From *Polacanthus* the present form differs in the whole surface of the ilium being covered in the former animal with a firm mosaic of very small, somewhat rounded, plates, which are scarcely at all sculptured, as I learn from Doctor Williston, who has examined the type specimen. These plates in *Stegopelta* are relatively quite large and strongly sculptured. The present form differs from *Polacanthus* also in the divergence of the points of the ilium anteriorly. In *Polacanthus* the iliac region was entirely covered by a bony shield, but in *Stegopelta* this shield was not continuous, but there was a space between the anterior ends of the ilia which was filled, probably, with small bony scutes. There have been many stegosaurian dinosaurs described from various parts of the world, notably North America and Europe. The group seems to have had a very wide distribution geographically.

In conclusion, I wish to express my gratitude to Dr. S. W. Williston, not only for his kindness in turning over the material to me for description but for his kindly interest and help during the entire investigation.

The specimen is in the Walker Museum, University of Chicago.

Since the above was written there have appeared two papers describing two new types of dinosaurian reptiles closely allied to the above-described form. One of these papers,* from the American Museum of Natural History, is of especial interest, since the material supplements in an excellent way that which has just been described. Mr. Brown's restoration of the *Ankylosaurus magniventris,* while based in large part on Marsh's drawing of *Stegosaurus ungulatus,* is not accurate as to the form of the animal. The pelvic region was undoubtedly covered over with a heavy shield as in *Stegopelta.* Indeed, Doctor Williston† says, "*Ankylosaurus* is either very closely allied to or identical with *Stegopelta* Williston, a genus overlooked by Mr. Brown."

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* Brown, Barnum, 1908. Bulletin Amer. Mus. of Nat. Hist., vol. XXIV, p. 187.

The remains described by Mr. Brown consisted of a skull, some small dermal scutes, a few vertebræ, a scapula, a few ribs and other parts, most of which were lacking in the above-described animal.

Dr. O. Abel has given (Verhandl. d. k. k. Zoöl.-bot. Gesell. in Wien, Bd. LVIII, p. 215, fig. 3) a restoration of *Ankylosaurus magniventris* Brown. It is to be doubted if he has added to our knowledge of dinosaurian attitudes, since the reader is at once struck with the grotesque and impossible attitude which he has caused the animal to assume. It is unfortunate that Brown's ideas of the arrangement of the scutes on the back should have been given by Doctor Abel, since there is not the slightest evidence that they assumed anything like the arrangement he has represented.

The other dinosaur is from the Niobrara Cretaceous of Kansas and was collected by Mr. Charles Sternberg in the Hackberry creek region.

Doctor Wieland‡ describes these remains as *Hierosaurus sternbergii,* new genus and species. This form is also doubtfully distinct from *Stegopelta,* unless it be that the skeletal characters were widely at variance to the characters of the dermal plates. A comparison of figure 9, plate LVI, of the present essay, with Doctor Wieland's figure 6, will show how very closely the dermal elements of the animals resemble each other. Comparisons also of the figures on plate LVII of the present paper with Doctor Wieland's figures 2, 4 and 5 will reveal the close similarity of the small dermal elements. It would, however, be too previous to say certainly that *Hierosaurus* and *Stegopelta* are identical. The geological horizon of the two specimens is certainly not far apart, or perhaps identical, since the Hailey shales occupy relatively the same position in Wyoming as the Niobrara chalk does in Kansas.

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† American Naturalist, vol. XLII, No. 501, p. 629.

‡ Wieland, G. R., 1909. Amer. Jour. Sci., March, p. 250.

BIBLIOGRAPHY.

1. WILLISTON, S. W. A New Armored Dinosaur from the Upper Cretaceous of Wyoming. Science, N. S., vol. XXII, No. 564, Oct. 20, 1905, p. 503.
2. News item, SCIENCE, N. S., vol. XXIV, No. 622, Nov. 30, 1906, p. 711.
3. DARTON, N. H. Geology of the Owl Creek Mountains. Senate document No. 219. Washington, D. C., 1906. Page 22.
4. LEIDY, JOSEPH. Notice of Remains of Extinct Reptiles and Fishes Discovered by Dr. F. V. Hayden in the Bad Lands of the Judith River, Nebraska Territory. Proc. Acad. Nat'l Sci., Phila., vol. VIII, pp. 72-73.
5. LEIDY, JOSEPH. Extinct Vertebrata from the Judith River and Great Lignite Formations of Nebraska. Trans. Amer. Philos. Soc., vol. XI, pp. 139-154, with plates VIII-XI. 1860.
6. DARTON, N. H. Geology of the Big Horn Mountains. Professional Paper No. 51, p. 55. Washington, D. C. 1906.
7. LAMBE, L. M. Contributions to Canadian Paleontology, vol. III, pt. II: On Vertebrata of the Mid-Cretaceous of the Northwest Territory. Art. No. 2: New Genera and Species from the Belly River Series. Geological Survey of Canada. 1902.
8. Contribution to Canadian Paleontology, vol. III, p. 57.
9. HULKE, J. W. Phil. Trans., 1881, p. 654, pl. 71, fig. 1.
10. OWEN, RICHARD. Monograph of the Fossil Reptilia of the Wealden Formation. Paleontographical Society, 1857, pl. V.
11. MARSH, O. C. The Dinosaurs of North America. 16th Ann. Rep. U. S. G. S., 1896, pl. LXXV, fig. 5.
12. HULKE, J. W. Phil. Trans., 1881, p. 655.
13. SEELEY, H. G. On the Os Pubis of Polacanthus foxii. Quart. Jour. Geol. Soc., vol. 48, pp. 81-95, pl. I.
14. HULKE, J. W. Phil. Trans., 1887, p. 171, pls. 8 and 9.
15. MARSH. Dinosaurs of N. A., 1896, pl. LXXIX, fig. 5.
16. Ibid, fig. 6.
17. LYDEKKER, RICHARD. On Part of the Pelvis of Polacanthus. Q. J. G. S., vol. XLVIII, pp. 148-149, with 2 figures.
18. HULKE, J. W. Q. J. G. S., vol. 30, pp. 516-518, pl. XXXI, figs. 1, 2.
19. HULKE. Phil. Trans., 1881, p. 657.
20. RICHARD OWEN. Monograph on Scelidosaurus, pt. II, Paleontographical Society, 1862, p. 20, pl. IX.
21. HULKE. 1881. Phil. Trans., p. 657, pl. 75, figs. 5, 6.
22. LAMBE. 1902. Contribution to Canadian Paleontology, vol. III, p. 56, pl. XXI, figs. 6, 7, 8.

23. HATCHER, J. B. 1905. Vertebrate Fauna of the Judith River Beds. Bull. U. S. G. S., pp. 67-103.

24. NOPSCA. 1905. Geol. Mag., N. S., Dec. 5, vol. II, p. 241.

25. SEELEY. 1881. Q. J. G. S., p. 653, pl. 31, fig. 3.

26. HUXLEY. 1867. Geol. Mag., vol. IV, p. 66, pl. V.

27. MARSH. 1896. Dinosaurs of North America, pl. LXX.

28. WILLISTON, S. W. American Amphicœlian Crocodiles, Jour. Geol., vol. XIV, No. 1, p. 1, 1906.

29. LAMBE. Contribution to Canadian Paleontology, vol. III, p. 56, pl. XII, figs. 3, 4, 1902.

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CONTENTS:

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A CONTRIBUTION TO THE SOFT ANATOMY OF CRETACEOUS FISHES AND A NEW PRIMITIVE HERRING-LIKE FISH FROM THE TEXAS CRETACEOUS.

BY ROY L. MOODIE.

(Contribution from the Zoölogical Laboratory, No. 191.)

Plates LX to LXII.

THERE have been, during the past few years, several additions to our knowledge of the soft parts of extinct animals. This knowledge has to do, in large part, with the firmer tissues, such as the cartilaginous portions of the skeleton, the skin, the muscles, but in some cases the kidneys, oviducts, nervous tissues, blood vessels and alimentary canal are clearly preserved. Dean (*1*) has been especially fortunate in the discovery of some of these structures in the sharks of the Cleveland shales of Ohio. He has described very fully the preservation of the kidneys, muscles, skin, the cartilaginous elements of the fins and arches and portions of undigested food. So perfectly are the remains preserved that the tissues, in some cases, admit of histological differentiations into the component elements. Eastman (*2*) has described the preservation of the outline of some acanthodians from Mazon Creek. Woodward (*3*) has contributed to our knowledge of the soft anatomy of fossil fishes in many ways and has added interesting information on the anatomy of the lateral line system of Cretaceous selachians. Jaekel (*4*), Dean (*1*, p. 267) and Gill (*5*) have discussed the anatomy and the significance of Jurassic and Cretaceous chimæroid egg cases. Otto Reis (*6*) has written much on the soft anatomy of various fossil fishes, more especially the Cœlacanthidæ, in which he has described the form of the muscle fibers, the swim bladder and other structures. Eastman and Parker (*21*) have described the preservation of the brain, the internal ear and arterial vessels in *Rhadinichthys deani* Eastman from the base of the Waverly shales, Kentucky. Dean (*20*) has mentioned the preservation of the lateral line sensory canals of the head, the auditory organ and the rim of the nasal capsule in *Acanthodes bronni* from the Permian of Lebach, preserved in the Berlin Museum. Fritsch (*7*) has described very accurately the outlines of the body and fin membranes of *Pleuracanthus*. Traquair (*8*), Dean (*1*) and Sollas (*9*) have added to our knowledge of the anatomy of *Paleospondylus*. Patten (*10*), Eastman, Traquair and others have written on various structures of the Ostracophores. Other authors have contributed from time to time on the subject, until we have, in some instances, *e. g., Bothriolepis, Paleospondylus, Cladoselache,* a fairly definite idea as to the outward form and internal structure of the creature. Among higher animals something has been done on the soft anatomy of the extinct Amphibia, Ichthyosauria, and Dinosauria.

It is with some degree of pleasure that the writer is able to add to the knowledge of the soft anatomy of extinct forms by the discussion of the alimentary canal of two Cretaceous fishes. One is a species of *Empo,* probably *E. nepaholica* Cope, from the Niobrara Cretaceous of western Kansas, and the other is a new species of clupeoid fish from the Cretaceous of Texas.

The specimen which probably belongs to *Empo nepaholica* Cope consists of the cast of a large stomach which, in all probability, represents a fish of some ten or twelve feet in length. It is No. 347 of the University of Kansas Paleontological Collection. The remains were discovered in 1897 by Mr. H. T. Martin in the Niobrara chalk four miles northwest of Elkader, Kan. The specimen has recently been presented to the Museum of the University by Mr. Martin.

The specimen consists of a cast of the larger portion of the alimentary canal of a large species of fish. Attached to the matrix of the cast on one side is the major portion of the right pectoral fin, which is described and figured below. So far as the writer is aware, the present specimen is the most perfect example of the pectoral limb of an *Empo* which has been described. Cope (*18a*) figured an incomplete one and Hay mentioned another. Hay (*11*) has figured a portion of the caudal fin of an *Empo* showing the extreme character of segmentation of the rays. The same character is shown in the pectoral fin.

The stomach is rounded, somewhat laterally compressed, and elongate in a slightly U-shaped curve. There are eight muscular constrictions on the ventral surface and four on the dorsal. The constrictions, on the ventral surface, occur in groups. Anteriorly there are two close together. This group is separated by a space of an inch and a quarter from the next group, in which there are three, which occur a little over one-half inch apart. The last group, also of three, is separated from the second group by one inch. The surface of the stomach cast is covered with a dark, apparently carbonaceous, material which may be carbonized muscle, together with a few large scales of the typical *Empo* form. Running the entire length of the specimen are longitudinal ridges and grooves showing the cast of the muscular walls of the stomach.

The interior of the stomach, in cross section, shows no food material, but only chalk. It is possible that the fish, like some of its modern relatives, may have been a bottom feeder and its stomach may have been partly filled with Niobrara mud at the time of its death. There must, however, have been some sediment enter the stomach after death, for the full form of the organ is preserved as though the entire stomach cavity had been packed with mud. Furthermore, the form of the stomach is that of a carnivorous fish, and recalls very strongly the stomach of a mountain trout or of the sunfishes of our inland streams, all carnivorous in habit.

The portion of the alimentary canal preserved is in two lobes. The first lobe is undoubtedly the stomach proper, and the constriction between the lobes is the pyloric region. The other lobe is unlike anything among modern fishes with which I am at present acquainted. It is undoubtedly an enlargement of the intestine and possibly served as a secondary stomach. It lacks the muscular constriction and the longitudinal plicæ. The plicæ are, however, continued well across the pyloric region to the beginning of this second enlargement.

The pectoral fin, as preserved, is well characterized in the photograph (plate LXII, figure 2). It is somewhat turned inward and bent, during interment, back against the stomach. There are eleven rays preserved. The anterior rays are cross segmented with long divisions, which measure 7 mm. in length in the second ray. The square notches mentioned by Hay (*11*, p. 87) as occurring on the specimen of *Empo nepaholica* Cope in the United States National Museum, are entirely lacking from that portion of the anterior ray which is preserved in the present specimen. The teeth on the edge are also absent, nor do I find that they are evident in Cope's figure referred to by Hay. The figure is very indistinct, and if the notches were present they could not, in the nature of the case, be normal, but would represent places where the segments had dropped out. The first ray is not a spine. In other respects the present specimen agrees well with that figured by Cope on plate LII, figure 1 (Cretaceous Vertebrata). The fifth and succeeding rays are segmented like the anterior ones, but the segments are smaller and measure, on the average, only about 2 mm. The seventh ray is especially broad, equaling in its proportions two and one-half of the other rays. All of the rays are split distally. The seventh divides into four secondary rays and the divisions ascend more and more to the base of the fin posteriorly. The fin supports are obscured by scales and matrix so that their nature cannot be determined. On the opposite side of the specimen, below the pectoral fin, there are large scales and fragments of ribs.

The second intestinal enlargement is interesting, entomologically, as showing the borings of some fossorial hymenopteron; possibly some one of the smaller species of the Andrenidæ. There are fragments of pupa cases in the burrows, so there is no doubt as to the recent origin of the holes.

The present specimen is so far the only remains known of the soft anatomy of the Kansas Cretaceous fishes, and, so far as I can learn, the first indication of the alimentary canal of Cretaceous bony fishes of any region. Whether the stomach and intestines in their various forms will ever be of any help in determining the relationship of the various osseous fishes remains to be determined. It is to be feared, however, that the fishes have been so diversified according to food habits that these structures will not be of any great phylogenetic value. The remains are interesting, however, as indicating, in a measure, the habits of life of at least one of the Cretaceous fishes.

Measurements of the specimen of *Empo nepaholica* Cope:

Entire length of the alimentary canal as preserved	53.2	cm.
Greatest diameter at anterior end	10	
Least diameter, across pyloric region	3	
Greatest diameter of posterior enlargement	7.4	
Length of pectoral fin as preserved	9	
Greatest width of fin	3.7	
Length of first ray	8	
Width of first ray	2	mm.
Diameter of large scale	15	

Thrissopater intestinalis new species.

A species of clupeoid fish is represented in the University Museum by the remains here described as a new species. The form is located in *Thrissopater* of Günther, described from the Gault of Folkstone in 1872 (*12*). My thanks are due Dr. A. Smith Woodward for the suggestion of a comparison of the present form with that of *Thrissopater*. It was thought for a time that the present form represented a genus distinct from *Thrissopater*. The distinguishing character was thought to be found in the position of the pelvic fins, which has served as a generic character in other fishes. In *Thrissopater salmoneus* the pelvic fin is opposite the dorsal and in the present form it is distinctly posterior to it. There is, however, a great range of variation in the position of the pelvic fin, especially among the lower osseus fishes. My thanks are due Prof. E. C. Starks for aid in reference to the characters of the modern bony fishes. During the summer of 1909 the writer spent some weeks studying with him the fishes of Puget Sound. He first called the writer's attention to the wide variation of the location of the pelvic fin in the clupeoid fishes. This variation is easily understood when it is remembered that the pelvic fin lies free from any firm attachment and hence its variation in location would not mean as much as though it were attached to the scapular arch. Further aid was rendered the writer in determining the characters of the clupeoid fishes by Dr. W. G. Ridewood, of London. An examination of the essays of this gentleman has been of great service.

The absence of material for direct comparison with the species of *Thrissopater* makes it best to locate the present form temporarily in that genus. The systematic position of *Thrissopater* has been the subject of a wide variance of opinion. Dr. Günther regarded *Thrissopater* as closely allied to the modern Clupeidæ and located it (*13*) in that family, in which he also included such forms as *Spaniodon, Albula, Elops* and *Engraulis*, all of which have been regarded by different authors as types of distinct families. Boulenger (*14*) regards *Thrissopater* as a member of the subfamily Thrissopatrinæ, which is one of his four subfamilies of the Clupeidæ. Dr. Jordan (*15*) located the form in the family Spaniodontidæ, which is closely related to the Elopidæ, between which and the Clupeidæ Boulenger regards *Thrissopater* as being intermediate (l. c., p. 564). Professor Starks writes me that Doctor Jordan now regards the family Spaniodontidæ as untenable. Dr. A. Smith Woodward (*16*) regards *Thrissopater* as a member of the Elopidæ, which differ from the Clupeidæ in the possession of a single supramaxillary, the degree of union of the parietals and the gape of the mouth and the presence of a gular plate. The present form presents the characters of the Elopidæ in so far as they are preserved. In recent forms, the presence of a gular plate in the Elopidæ serves as a convenient landmark for the distinction of the families of the Elopidæ and Clupeidæ. As a matter of fact, the families are so closely allied that the characters used for their separation must in time be broken down by the discovery of new material.

Herrings and herring-like fishes are not at all rare in the Cretaceous deposits of the world. Davis (*17*) has described many forms of clupeoid fishes from Mount Lebanon. Before him Agassiz advanced the knowledge of these forms, and latterly Woodward has described several interesting clupeoids. Cope described several clupeoids from the Eocene of Green River, Wyoming (*18*), and Jordan has cited the interesting relations of these forms to forms now living in the rivers of Australia and Chili. At the present time herrings form an important item in the economic history of the world. Huxley has dwelt (*19*) especially on the anatomy and relations of the herring in this connection. The present form adds yet another mite to our knowledge of these interesting fishes. It is believed to be as early as or perhaps somewhat older than many of the described clupeoids. The specimen comes from the Austin shales or limestone, which is a probable equivalent of the Niobrara Cretaceous. It is from near Baylor, Tex., and is No. 300 of the University of Kansas Museum.

The remains preserved consist of the nearly complete fish, as may be determined from an examination of the plate. The caudal portion is, unfortunately, lacking. The outer surface of the skull was badly broken and Mr. Martin very kindly extricated the skull for me from the matrix. It was a difficult task and the results were hardly worth the efforts, for the embedded portion was but little better preserved than the outer. Enough of the skull is preserved, however, to show many of the important characters. The head is naked; the body compressed, but whether the ventral edge was drawn out into a keel or not cannot be determined from the specimen. The mandible is fully as long as the skull. The relations of the articulation to the orbit cannot be determined, nor can the position of these openings be definitely located. The parietal bones are, apparently, small. Certainly the supraoccipital projects forward as in *Thrissopater magnus.* Maxilla is slender, with a single supramaxillary. The margin of the jaws is provided with a single row of small, recurved, sharply pointed teeth of uniform size throughout the length of the entire mandible and maxilla. The quadrate is broadly V-shaped, with a prominent articular surface. Nasal, ethmoid and premaxillary bones ornamented with numerous small pits. The same character occurs on the anterior end of the maxilla of the right side. A single, squarish, punctate, thick, pharyngeal bone is present. A very few branchiostegal rays are preserved; not over ten. From the relationships of the form we would judge there were many in the complete fish. The opercular apparatus is smooth. Posterior suborbital plate radiately furrowed; its extent exceeding one-third of the length of the skull; remaining elements indistinct. Greatest depth of the body is slightly greater than the length of the skull from premaxilla to supraoccipital. The length of the body is possibly equal to four times the length of the skull. The fins are relatively small. Dorsal fin median in position. The pectoral fin has sixteen rays, which are cross-segmented but are not divided longitudinally. The rays are supported by five baseosts. The distance between the origins of the pectoral and pelvic fins is equal to nearly four times the length of the pectoral fin. The pelvic fins have nine rays, none of which are cross-segmented. The pelvic bone is large and spatulate.

The body scales are small, cycloid, deeply imbricated and marked with fine concentric lines. There is a large, elongated and elegantly sculptured scale at the base of the pectoral fin, as in *Thrissopater salmoneus;* though in the present instance the scale is less than one-half the length of the pectoral fin rays. The vertebræ are preserved to the number of thirtyfour. There may have been as many as forty-five or fifty in the complete fish. They are fully ossified, slightly constricted and marked with small longitudinal ridges. The length is slightly greater than the depth. The neural spines are long and interlock with the interneurals. Supernumerary ribs present. Six of them occupy the space of a single vertebral centrum.

The specimen as preserved is well characterized by the figures. The fish lacks the posterior end of the body back of the anus. It is chiefly remarkable on account of the extraordinary preservation of the casts of the rectum and intestine, of which there are six coils or loops preserved. The remains are embedded on the right side in a calcareous, arenaceous, shaley limestone, which also contains remains of some species of *Inoceramus*, small fish teeth and the base of a moderately large shark's tooth.

Perhaps the most interesting portion of the entire specimen is the intestinal canal, from the presence of which is derived the specific name. In general features the alimentary canal as preserved recalls that of the common fresh-water buffalo fish, *Ictiobus bubalus* Raf (plate LXII, figure 1). The similarity in form is undoubtedly indicative of similarity of habit, and since we know that the buffalo fishes are bottom feeders we can easily predicate that our ancient Cretaceous fish had similar habits and at the time of its death the alimentary canal was filled with mud mixed with some organic substances; for the fossil shows a different texture for the cast of the alimentary canal from the matrix, indicating different materials. The intestine as preserved consists of six coils or loops of the very small intestine which immediately precedes the rectum, which is likewise preserved. The rectum is elongate but no more so than is the same structure in the buffalo fish. The essential characters are shown in the illustrations.

The distinction of this species from the other three which have been assigned to *Thrissopater* is to be found, first of all, in the posterior location of the pelvic fin. Its base lies at a distance posterior to the back edge of the dorsal fin, which is equal to its own length. So far as I am aware the large axillary scale in other species of *Thrissopater* is larger and unornamented. From *T. salmoneus* Günther the present form is to be distinguished by the relative proportions of the head and body. The head and opercular apparatus is contained only about twice or at most two and one-half times in the body. From *T. magnus* it is to be differentiated by the relative proportions of the opercular and the skull. The former is contained twice in the latter in the present form. In *T. magnus* it is contained three times. The present species is indeed very closely allied to *Thrissopater magnus* Woodward from the Lower Chalk of Hollingbourn, Kent. It is to be distinguished by the relative dimensions of the vertebræ as well as by the proportions existing between skull and opercular. The vertebræ in *T. magnus* are higher than long while in *T. intestinalis* they are slightly longer than high, and the ends are occupied by distinct rims, such as do not occur, apparently, in the English form. The characters which the two species have in common are striking. They both have the same notch in the anterior end of the mandible; the same finely punctate ethmoid and nasals; the same form and dimensions of mandible and maxilla; the same divided posterior suborbital; and the same relative shape of skull. Many of these are generic characters.

The present species can be distinguished from *Thrissopater* (?) *megalops* Woodward by the proportions of the head. In *T.* (?) *megalops* the height of skull from cotylus to supraoccipital is equal to the length of the mandible, while in *T. istestinalis* the mandible exceeds the height of the skull from cotylus to supraoccipital by 15 millimeters. It may be further distinguished by the relative proportions of the pectoral arch and skull as well as by the absence of the radiately furrowed suborbital and the notch in the anterior end of the mandible in *T.* (?) *megalops.*

Measurements of *Thrissopater intestinalis* Moodie:

Length of specimen	29	cm.
Greatest depth	9	
Length of skull (with opercular apparatus)	9.7	
Depth of skull at quadrate	4.8	
Length of mandible	6	
Depth of mandible at cotylus	1	
Diameter of pharyngeal plate	9	mm.
Length of tooth	2.5	
Width of opercular apparatus	3	cm.
Length of clavicle	2.5	
Length of pectoral fin	2.5	
Width of pecoral fin	1.2	
Length of pelvic fin	2.4	
Width of pelvic fin	1.2	
Length of actinost	3	mm.
Length of dorsal fin as preserved	2.1	cm.

Width of dorsal fin as preserved	1.8	
Length of caudal hæmapophyses	9	mm.
Length of vertebræ	6	
Depth of vertebræ	5	
Width of small intestine	3	
Length of rectum	12	cm.
Width of rectum	1.3	
Length of interneural	1	

BIBLIOGRAPHY.

1. **Dean, Bashford**, 1909. Studies on Fossil Fishes (Sharks, Chimæroids and Arthrodires). Memoirs of the American Museum of Natural History, vol. IX, part V, pp. 211-287, with 65 text-figures and plates XXVI-XLI.

1*a*. **Hussakof, Louis**, has given a very full bibliography of the forms here discussed. Studies on Arthrodira, Memoirs of the American Museum, 1906, vol. IX, part III.

2. **Eastman, Charles R.**, 1902. The Carboniferous Fish Fauna of Mazon Creek, Journal of Geology, vol. X, p. 536.

3. **Woodward, A. S.**, 1888, Paleontological Contributions to Selachian Morphology, I: On the Lateral Line of Cretaceous Species of Scyllidæ. Proc. Zool. Society of London, p. 126.

——— 1898. Preliminary Note on a New Specimen of Squatina from the Lithographic Stone of Nusplingen, Würtemberg. Geological Magazine, December, IV, vol. V, No. 409.

3*a*. **Colline, W. E.**, 1895. The Morphology of the Sensory Canal System in Some Fossil Fishes. Proc. Birmingham Phil. Soc., vol. IX.

4. **Jaekel, Otto**, 1901. Ueber jurassiche Zähne und Eier von Chimæriden. Beilage Band Neues Jahrbuch f. Mineralogie, etc., Bd. 14, pp. 540-564, fig. 3, Tafeln XXII-XXIII.

5. **Gill, Theodore**, 1905. An Interesting Cretaceous Chimæroid Egg-case. Science, N. S., vol. XXII, No. 567, p. 601, November 10.

6. **Reis, Otto**, 1888. Die Cœlacanthiden. Paleontographica, Bd. XXXV, pp. 1-96, Tafeln I-V.

Reis, Otto, 1889. Ueber ein Art Fossilization der Muskulatur. Gesellschaft f. Morphologie u. Physiologie in Muenchen, pp. 1-6.

Reis, Otto, 1894. Ueber Phosphoritisirung von Cutis der Testikel und des Ruckenmarks bei fossilen Fischen. Archiv f. Mikro. Anatomie, Bd. 44, pp. 87-119.

Reis, Otto, 1898. Neues ueber petrificirte Muskulatur. Archiv f. Mikros. Anatomie Bd. 52, pp. 262-268.

7. **Fritsch, Anton**, 1895. Fauna der Gaskohle und der Kalksteine der Permformation Bohmens, vol. III, p. 1.

8. **Traquair, R. H.** See bibliography in reference No. 9.

9. **Sollas, W. J. and I. B. J.**, 1904. An Account of the Devonian Fish, *Palæospondylus gunni* Traquair. Phil. Trans. Royal Society, London, vol. 196, B, pp. 267-294, plates 16-17.

10. **Eastman, Chas.** The results of Patten, Traquair, Dean, Eastman and others are very adequately discussed in Eastman's two memoirs:

Devonic Fishes of the New York Formations, Memoir No. 10 of the New York State Museum, pp. 24-65;

Devonian Fishes of Iowa. Annual Report Iowa Geological Survey, vol. XVIII, pp. 31-291; 41 text-figures, plates I-XVI. 1907.

11. **Hay, O. P.**, 1903. On Certain Genera and Species of North American Cretaceous Actinopterous Fishes. Bull. Amer. Mus. Nat. History, vol. XIX, p. 88, plate I, fig. 4.

12. GUNTHER, A., 1872. Figures and Descriptions of British Organic Remains. December. XIII, Mem. Geol. Survey No. 1, plate I.

13. GUNTHER, A., 1880. The Study of Fishes, p. 656.

14. CAMBRIDGE NATURAL HISTORY, vol. 7. Boulenger, Systematic Account of the Teleostei, pp. 562-564.

15. JORDAN, D. S. Guide to the Study of Fishes, vol. II, p. 43.

16. WOODWARD, A. S., 1901. Catalogue of Fossil Fishes of the British Museum, part IV., page 32, plate V, fig. 1, VII, fig. 4.

17. DAVIS, J. W., 1887. The Fossil Fishes of the Chalk of Mount Lebanon, in Syria. The Scientific Trans. Roy. Dublin Society, vol. III (ser. II), art. XII, p. 567, plates XXXI-XXXIV.

18. COPE, E. D., 1884. Tertiary Vertebrata, book I, p. 77, plate IX.

18*a*. COPE, E. D., Cretaceous Vertebrata, plate LII, fig. 1.

19. HUXLEY, T. H., 1881. The Herring, Scientific Memoirs, IV, pp. 473-492.

20. DEAN, BASHFORD, 1907. American Jour. Anatomy, VII, p. 218.

21. EASTMAN, C. R., 1908. The Devonian Fishes of Iowa, vol. XVIII, Iowa Geol. Survey, pp. 264-272. Article by Dr. G. H. Parker on the "Auditory Organs and Other Soft Parts," on p. 272.

THE

KANSAS UNIVERSITY SCIENCE BULLETIN.

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(Whole Series, Vol. XV, No. 16.)

CONTENTS:

A New Species of Holotrich, ... *By Nadine Nowlin.*

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THE KANSAS UNIVERSITY SCIENCE BULLETIN.

VOL. V, No. 16.] MARCH, 1910. [WHOLE SERIES VOL. XV, NO. 16

A NEW SPECIES OF HOLOTRICH.

BY NADINE NOWLIN.

(Contribution from the Zoölogical Laboratory, No. 193.)

Two text figures.

IN April of 1909 there was brought to my room at the Naples Station a jar of the small barnacle *Lepas pectinata,* and in examining microscopically one of the appendages I observed a minute rotifer-like animal creeping along its edge. This animal, after being studied for some time, was found to be an infusorian—a Holotrich, resembling in a general way Huxley's *Dysteria armata.* Upon careful study, however, it differed in so many ways that I concluded it to be a distinct form.

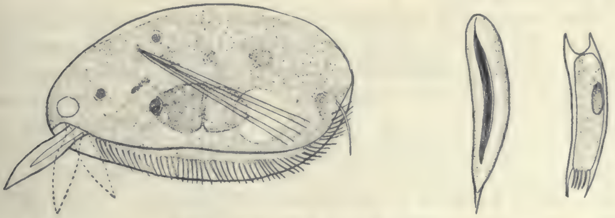
Symbiosis is such an old and well known condition in the organic world that any discussion of it for its own sake is unnecessary here. As in other cases, these two animals live together, deriving mutual benefit from the combination; the ciliate finding a shelter in the appendages and the barnacle, no doubt, getting a tasty morsel when it succeeds in dislodging the little animal long enough to sweep it into the gullet. It is a question how the protozoön manages to thrive under these conditions. We know that the water currents set up by the host are swift and frequent, and life under such tempestuous conditions would seem worse even than the chances in the open sea. The structure of the smaller organism partially explains this. It has first of all an armature, a tough siliceous skeleton, covering the body, except a narrow strip on the ventral side. With this protection it is not easily crushed. Then caudally there protrudes a hook-like tail, which not only helps the animal in creeping over the rough surface of the appendage, but also serves as an efficient means of attachment. Near the oral opening protrudes a long flagellum which lashes rapidly to and fro and secures food for the animal.

The small visitor thus established on the appendage of a barnacle obtains its food from the currents of water which are constantly coming in to the host. When the dangers come and the appendages are enclosed by the calcareous plates of the barnacle, the ciliate still has moisture and some food. One might think that in casting its lot with a sedentary animal the free-swimming protozoön had limited its opportunities. This is not wholly true. *Lepas pectinata* grows on masses of lava, and during storm these masses become broken and widely scattered. It is only occasionally that the Naples collectors are able to find this barnacle—its appearance in the bay depending upon, first, a storm at sea, and then a strong south wind to sweep it in. During April and part of May I was able to obtain this material but twice. This was unfortunate as the nucleus is an interesting one, and promises well for cytological work. The barnacles live less than a week indoors and the ciliates perish with them. Moreover, the ciliates are not numerous. As a last resort for material, I took barnacles from the storeroom, preserved in formalin, and succeeded in finding the specimens, but they did not prove satisfactory for nuclear study.

DESCRIPTION OF SPECIMEN.

The animal is oval in form, being slightly wider cephalically. It is covered with siliceous skeleton, giving the appearance of a bivalve shell, and possesses a caudal appendage. So different is it from the usual infusor that it is little wonder most zoölogists at first glance pronounce it a rotifer, or a mollusk, or a low crustacean. The animal is flattened dorso-ventrally, the dorsal shell being more extensive and bending over the right side. The dorsal is slightly convex; the ventral is concave and attaches to the dorsal by a deep groove on the left. The right edge of the dorsal shell and the left edge of the ventral do not meet, thus leaving exposed a very narrow strip of protoplasm. This uncovered protoplasm is ciliated and it is by means of these cilia that the animal swims. The surface of both shells is smooth.

The crevice between the ventral and dorsal plate lies then on the right ventral area of the animal, and because the animal moves often on the edge we are apt to think of this ciliated region as purely ventral. Lankeste in describing the family Dysterina, to which I believe this specimen belongs, calls this the ventral side. The right ventral groove then extends from the posterior end of the animal completely along the side and rounds across the cephalic end. At its caudal extremity is an appendage, and at the cephalic, a long flagellum.



EXPLANATION OF TEXT FIGURES.

The figure to the left is a view of the right dorsal side of the animal, showing the flagellum anteriorly and the ventral cilia; the calcareous supporting rods of the mouth, the two contractile vacuoles and the nucleus. The caudal appendage is shown by a continuous line and its range of motion by dotted lines.

The middle figure is a view of the animal on edge, showing a convex dorsal side, concave ventral, left dorsal groove and caudal appendage.

The right figure is an imaginary cross-section through the nucleus.

The tail, like the body, is covered by the silicious skeleton and appears hollow, at least part of the way. Whether the anus lies at its distal end, as is claimed for *Onychodactylus*, I am unable to say. Its range of movement is nearly 180 degrees in the plane of the right ventral groove. In movement the animal may use this organ as a propeller, shoving itself forward with long strides by placing the end against a solid structure. It is this motion which resembles strongly that of a rotifer. In swimming the tail is usually folded into the groove like a knife-blade closed in its handle, and the animal is carried forward by the vibration of its cilia. The animal when creeping over a solid surface stands on the ciliated edge, much as a mussel when moving through the sand. In swimming it lies slightly on its ventral side and has a swinging motion through the water.

The flagellum is located in a deep depression of the cephalic protoplasm. On superficial examination this depression might be mistaken for the mouth, but the mouth is just ventral to it and convenient to the currents set up by the flagellum.

The gullet is a long, narrow funnel running obliquely upwards and backwards until it nearly reaches the opposite side of the body. Like other protozoa of this group, it is supported by calcareous rods. These are plainly visible when picrosulphuric acid is first placed on the specimen, but very soon the acid destroys them and the gullet shows only as a clear place in the protoplasm.

Two contractile vacuoles are present, and a very large nucleus. The nucleus is especially interesting in these forms because the meganucleus is heterogeneous, the anterior half remaining almost clear when stained with picro carmine, the posterior half staining densely. The micronucleus may lie quite far to the posterior end of the meganucleus. The fact that the two halves of the nucleus react differently to the same stain suggests a segregation of functions. Since in division the meganucleus breaks transversely, the resulting animals are dimorphic as to meganuclear protoplasm.

CLASSIFICATION.

According to Lankester's classification the specimen described above belongs to the sub-order Gymnostomata, that division of the Holotrichs in which the mouth is closed in the intervals between the acts of ingesting food. It belongs to the family Dysterinæ (Clap. & Lach.), which corresponds to Calkins's sub-family Ervilinæ: Cilia confined to ventral surface or a portion of it; caudal end invariably possesses a movable style arising from caudo-ventral surface.

Of the various genera grouped under this family, or subfamily, our specimen corresponds most closely to the last of the following list:

Ægyria (Clap. & Lach.), 1858.
Onychodactylus, Entz, 1884.
Trochilia, Duj., 1841.
Dysteria, Huxley, 1857.
Dysteropsis, Roux, 1902.

The only species of this genus, so far as I can learn, is the small one found in the lakes of Geneva and called minuta by Roux, because it measures only 28 micra long and 16 micra wide. The animal described in this paper is marine; the average specimen is 83 micra long and 50 wide. Its habitat in the tentacles of *Lepas pectinata* suggests the name of *Dysteropsis pectinata* for the new specimen.

BIBLIOGRAPHY.

Bronn, H. G. 1880. Klassen und Ordnungen des Thier Reichs, vols. I, II, III.

Claparede and **Lachmann.** 1850-'60. Etudes sur les Infusoires et les Rhizopodes. Mem. Inst. Genevoise, 5, 6, 7.

Calkins, G. N. 1902. Marine Protozoa from Woods Hole. Bull. U. S. Fish Comm. 21, pp. 415-468.

Calkins, G. N. 1909. Protozoology. Lea & Febriger.

Huxley, Thos. 1857. Mic. Trans. Jour., vol. 5.

Lankester, Eray. Protozoology, part 1, fascicle 2.

Roux, Jean. 1899. Infusoires cilies des environs de Geneve. Rev. Suisse, Zool. 6.

Roux, Jean. 1901. Faunne Infusoirenne des eaux stagnents des environs de Geneve. Mem. cour. de l'Universite de Geneve.

Roux, Jean. 1901. Faunne Infusoirienne des environs de Geneve. Vehr. Zool. Congr. 5 (Berlin).

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CONTENTS:

ORTHOPTERA FROM THE SANTA RITA MOUNTAINS, ARIZONA, COLLECTED BY THE UNIVERSITY OF KANSAS EXPEDITION, *James A. G. Rehn.*

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ORTHOPTERA FROM THE SANTA RITA MOUNTAINS, ARIZONA, COLLECTED BY THE UNIVERSITY OF KANSAS EXPEDITION.

BY JAMES A. G. REHN.
Academy of Natural Sciences of Philadelphia.

Plate LXIII.

THE collection forming the basis of this paper was made in the Santa Rita range during the summer of 1907 by the University Museum expedition under the late Prof. F. H. Snow.

FORFICULIDÆ.

Spongophora apicidentata Caudell.

Santa Rita mountains, 5000 to 8000 feet, July. F. H. Snow. One female.

This species has previously been recorded from localities in Arizona ranging from near a hundred feet to about five thousand feet above sea level.

BLATTIDÆ.

Ischnoptera notha Rehn and Hebard.

Santa Rita mountains, 5000 to 8000 feet, July. F. H. Snow. One female.

This specimen agrees with an individual of the same sex from the Huachuca mountains previously examined by the author.*

The measurements of the Santa Rita specimen are as follows:

Length of body	14.0 mm.
Length of pronotum	4.5
Greatest width of pronotum	5.9
Greatest width of tegmen	4.5
Length of tegmen	10.0

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* Proc. Acad. Nat. Sci. Phila., 1907, p. 25 (*Uhleriana*); Rehn and Hebard, Ibid. 1910, p. 443.

In Arizona this species appears to be restricted to certain elevations on mountains of the southern part of the territory, viz., Santa Rita, Huachuca and Patagonia ranges.

Blattella dilatata (Saussure).

Santa Rita mountains, 5000 to 8000 feet, July. F. H. Snow. One female, one male.

These specimens agree with those recorded by the author* from the Huachuca mountains.

MANTIDÆ.

Bactromantis virga Scudder.

Santa Rita mountains, 5000 to 8000 feet, July. F. H. Snow. One female.

This specimen is slightly larger than a Huachuca mountains individual of the same sex.

PHASMIDÆ.

Pseudosermyle truncata Caudell.

Santa Rita mountains, 5000 to 8000 feet, July. F. H. Snow. One female.

Parabacillus coloradus Scudder.

Santa Rita mountains, 5000 to 8000 feet, June. F. H. Snow. Two males, one female.

ACRIDIDÆ.

Telmatettix aztecus Saussure.

Santa Rita mountains, 5000 to 8000 feet, June. F. H. Snow. One male.

Mermiria texana Bruner.

Santa Rita mountains, 5000 to 8000 feet, July. F. H. Snow. One female.

Prorocorypha,[1] n. gen.

Allied to *Paropomala* Scudder, but differing chiefly in the great development of the cephalic portion of the head, the greatly elongate supra-anal plate of both sexes and the subgenital plate of the male.

Body sub-bacilliform. Head greatly elongate; vertex and pre-ocular region strongly produced into a rostrate process, fastigium lanceolate, tectate, carinate; antennæ, at least of male, somewhat triquetrous, subensiform. Cephalic and median limbs very small. Caudal limbs very slender. Prosternum with a median compressed protuberance; mesosternal lobes contiguous. Supra-anal plate aculeate in both sexes; subgenital plate of male strongly produced, knife-like.

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* Proc. Acad. Nat. Sci. Phila., 1907, p. 26.

[1] πρωα, prow; κορυφη, head.

Type: *P. snowi*, n. sp.

Prorocorypha snowi n. sp. (Plate 63.)

Types: ♂ and ♀ (not mature); Santa Rita mountains, Pima and Santa Cruz counties, Arizona, 5000 to 8000 feet, June (♂), July (♀), 1907. F. H. Snow. (University of Kansas.)

Size medium; form very elongate. Head one and one-half times the dorsal length of the pronotum, occiput with a hardly perceptible longitudinal arcuation; interocular region but little narrower than the greatest width of the fastigium; rostrum very long and deep, occupying nearly half the length of the head and the greater part of the depth; outline when seen from the side with fastigium slightly ascending from the interocular region, face nearly horizontal, inter-antennal portion rounded to the acute angulate fronto-fastigial angle; fastigium lanceolate, the greatest width contained twice (♂) or more than twice (♀) in the length, apex very narrowly rounded, lateral margins distinctly carinate, surface tectate, median carina as distinct as the lateral and extending to the inter-antennal region; lateral foveolæ very elongate, lanceolate; frontal costa narrow, very slightly but regularly expanding ventrad in the male, very narrow dorsad, expanding somewhat in the inter-antennal region and subequal ventrad in the female, in both sexes moderately sulcate and becoming obsolete before reaching the clypeal margin; eyes flattened, elongate ovate, not at all prominent; antennæ, in the male at least, slightly exceeding the head and entire thorax in length, thick, three-sided, one narrower than the others, ensiform. Pronotum about twice as long as its width, cephalic margin of dorsum truncato-rotundate, caudal margin truncate, median carina distinct; lateral lobes with the ventral margin truncate. Wings and tegmina undeveloped. Prosternum with a very distinct longitudinal rounded tubercle; mesosternal foramina considerably impressed. Abdomen with the segments considerably elongate; supra-anal plate in both sexes strongly produced, needle-like, its length being but very slightly less than the dorsal length of the pronotum; cerci somewhat compressed, simple, sub-styliform; subgenital plate of male produced into a compressed, slightly arcuate knife-like structure, slightly more than half again as long as the supra-anal plate; ovipositor jaws of the female placed well under the projecting supra-anal plate. Cephalic and median limbs very small; caudal femora reaching to the fifth abdominal segment, very slender, tapering; caudal tibiæ equal to the femora in length, armed on the external margin with fourteen to sixteen small spines.

General colors of female burnt carmine and apple green, the venter of the body and head ochraceous, the carmine strongest on the dorsum, the green only on the limbs; caudal femora yellowish proximad. Color of male destroyed by immersion in liquid preservative.

MEASUREMENTS.

	Male.	*Female.*
Length of body (including subgenital and supra-anal plates)	31.0 mm.	44.0 mm.
Length of head	5.5	7.2
Length of fastigium	2.7	3.8
Length of pronotum	3.2	5.0
Length of caudal femur	10.5	13.6
Length of supra-anal plate	3.4	4.4
Length of subgenital plate	5.0	

A single pair have been examined. Doctor McClung, of the University of Kansas, who has studied the spermatogenesis of this species and whose assistants collected specimens under Professor Snow, informs me that "specimens such as those you have were constantly caught *in copulo*, and a microscopical examination of the testes shows the spermatozoa well developed." The specimens in hand have the tegmina and wing pads in the reversed nymphal condition.

Eritettix variabilis (Bruner).

Santa Rita mountains, 5000 to 8000 feet, June and July. 1907. F. H. Snow. One male, four females.

One of the females in this series is in a greenish phase of coloration, while two of the remaining females have a pattern of chiefly solid contrasting colors. The green phase has the greater part of the head, dorsal half of the lateral lobes of the pronotum, the pale stripe on the tegmina and the dorsal face of the caudal femora apple green, while the strongly contrasted phase has broad seal brown postocular bars extending over the head and pronotum and regularly expanding in width, the dorsal aspect much lighter, either ochraceous or rust red, and the usual dark portions of the tegmina also seal brown. The supplementary carinæ of the pronotum are distinctly but not strongly indicated in two of the females, represented by the merest traces in the female and completely absent in the two contrasting colored females.

The only previous Arizona record of this species is from Douglas, Cochise county.

Amphitornus ornatus McNeill.

Santa Rita mountains, 5000 to 8000 feet, June and July, 1907. F. H. Snow. One male, one female.

Cordillacris pima Rehn.

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One male.

This species was known only from the Baboquivari mountains, Pima county, Arizona.

Psolœssa texana Scudder.

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One female.

This specimen is in the blackish phase of coloration—the typical *texana* form.

Aulocara femoratum Scudder.

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One male.

This species is now known in Arizona from the Huachuca and Santa Rita mountains, and from Phœnix.

Arphia aberrans Bruner.

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One male, one female.

This species is now known from localities extending from the Huachuca range to Nogales, Ariz.

Hippiscus corallipes (Haldeman).

Santa Rita mountains, 5000 to 8000 feet, June and July, 1907. F. H. Snow. One male, one female.

Scirtetica ritensis, n. sp. (Plate 63.)

Type: ♀; Santa Rita mountains, Pima and Santa Cruz counties, Arizona. Elevation, 5000 to 8000 feet. July, 1907. F. H. Snow. (University of Kansas.)

A very beautiful species of the genus, differing from its allies in the absence of a median band on the wings, the dark color being on the periphery, in the color of the disk and in the heavy, robust build.

Size medium; form robust. Head with the extreme width very slightly greater than the greatest width of the cephalic margin of the pronotum; occiput slightly arcuate longitudinally, the caudal section of vertex with a pair of distinctly impressed subpyriform areas; interocular region slightly wider than the fastigium, broadly and deeply sulcate; fastigium very greatly declivent, sulcate as in the interocular space, the sulcate portion, however, being slightly broader than between the eyes; frontal costa somewhat narrower than the fastigium dorsad, very gradually expanding ventrad to very near the clypeal suture, where the margins curve strongly laterad, sulcate ventrad to immediately dorsad of the ocellus, where the sulcus terminates abruptly, and from the ocellus ventrad it is present shallower and sub-obsolete as the clypeal suture is approached; lateral foveolæ lanceolate, trigonal, distinctly impressed; eyes broad, somewhat depressed ovoid in outline, about equal in length to the infra-ocular groove, moderately prominent when viewed from the dorsum; antennæ about equal to the dorsal length of the head and pronotum; ventral portion of head distinctly broader than the dorsal. Pronotum with the length of the disk about half again the dorsal length of the head, and with the greatest width of the disk but slightly shorter than the length; cephalic dorsal margin very slightly obtuse-angulate, caudal margin decidedly obtuse-angulate; lateral angles of the disk very distinct on the metazona and the cephalic portion of the prozona, broken and sub-obsolete mesad; median carina distinct, moderately elevated, straight, cut by the transverse sulcus very slightly cephalad of the middle; lateral lobes distinctly deeper than long, the cephalic and caudal margins obliquely emarginato-sinuate, ventro-caudal angle broadly rounded. Tegmina exceeding the tips of the caudal femora by slightly more than the length of the pronotum, moderately broad, slightly narrowing distad, the apex obliquely rotundato-truncate; intercalary vein prominent, through the greater part of its length closer to the median than to the ulnar vein. Wing with the greatest width contained one and one-thirds times in the length, apex sub-rectangulate with the distal portion of the costal margin arcuate. Mesosternal lobes with the interspace very strongly transverse; interspace between the metasternal lobes transverse. Caudal femora robust, the ventro-lateral carina distinctly lamellate, reaching its greatest expansion at two-fifths the distance from the apex, pattern of the paginæ distinct; caudal tibiæ slightly shorter than the femora, armed laterad with seven spines.

General colors vandyke brown and pea green, marbled and blotched one over the other, the tegmina, dorsal face of the caudal femora and disk of the pronotum with the green predominating; ventral surface isabella color. Dorsum of the head and pronotum with a regular figure of green which is margined laterad with clove brown, this figure being constricted at the caudal margin of the head and almost severed mesad on the pronotum; antennæ clove brown annulate with pea green, their insertion bordered dorsad and ventrad by a pair of transverse lines of clove brown; eye walnut brown. Wings with the disk orange rufous, the distal and caudal margins with a moderately broad band of vandyke brown which fails to reach the proximal margin, ulnar tænia extending about half way to the base of the wing; apex with the smaller areas and a few of the short veins creamy white. Caudal femora with the dorsal face crossed by a median and a disto-median bar of clove brown, while the apex is touched with the same color, ventral sulcus washed with pale blue; caudal tibiæ turquoise blue with the lateral face of the proximal third greenish white and the extreme distal portion of the internal face blackish, leaving a pregenicular pale annulus, the apex dark blue, and a dark blue annulus placed next to the pale one; tarsal joints very pale ochraceous.

MEASUREMENTS.

Length of body	23.8 mm.
Length of pronotum	4.5
Length of caudal femur	12.0
Length of tegmen	21.0

The type specimen is the only one seen by the author.

Tomonotus aztecus (Saussure).

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One male.

Mestobregma rubripenne (Bruner).

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One male, one female.

Conozoa carinata Rehn.

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One female.

Trimerotropis alliciens (Scudder).

Santa Rita mountains, 5000 to 8000 feet, June and July, 1907. F. H. Snow. Three males.

These specimens are somewhat smaller than a female from the Huachuca mountains.

Trimerotropis laticincta (Saussure).

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One male, one female.

This species has previously been recorded from Nogales, Douglas and the Huachuca mountains in southern Arizona, and Flagstaff in northern Arizona.

Trimerotropis cyaneipennis (Bruner).

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One female.

Heliastus benjamini Caudell.

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One female.

This specimen has pale interrupted decussate markings on the pronotum.

Previous records of this species are from the Huachuca mountains, the Baboquivari mountains, and Nogales, Ariz.

Heliastus aridus (Bruner).

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One male.

Dactylotum variegatum (Scudder).

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. Two females.

TETTIGONIDÆ.

Arethæa sellata Rehn.

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One male.

This is the first record of the species outside of the Huachuca mountains.

Scudderia furcifera (Scudder).

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. One male.

GRYLLIDÆ.

Gryllus alogus Rehn.

Santa Rita mountains, 5000 to 8000 feet, July, 1907. F. H. Snow. Two females.

These specimens measure as follows:

Length of Pronotum.	*Tegmen.*	*Caudal femur.*	*Ovipositor.*
4.0 mm.	9.0 mm.	12 mm.	14.5 mm.
3.3	5.5	11	13.8

This species has been recorded from the Huachuca mountains and Phœnix, in addition to Albuquerque, the type locality.

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CONTENTS:

OBSERVATIONS ON THE GRYLLIDÆ: III. NOTES ON THE CLASSIFICATION AND ON SOME HABITS OF CERTAIN CRICKETS, *W. J. Baumgartner.*

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OBSERVATIONS ON THE GRYLLIDÆ: III. NOTES ON THE CLASSIFICATION AND ON SOME HABITS OF CERTAIN CRICKETS.

BY W. J. BAUMGARTNER.

(Contribution from the Zoölogical Laboratory, No. 195.)

CLASSIFICATION.

IN the course of collecting material for some cytological studies on the crickets, I was early confronted with the question of what are the true species of *Gryllus*. The first specimens collected I (*2*) called *Gryllus assimilis*, after carefully comparing them with the labeled specimens in the University of Kansas collection, and after reading such descriptions as were then available in the library. Later I collected about Chicago, Ill., and Woods Hole, Mass. My attempts at classifying these specimens led me to the conclusion that the species of *Gryllus*, the common larger field crickets, are not fixed but grade into each other. I found that in all of these places there were two groups with different breeding seasons—one that passed the winter in the nymph stage, and another that passed it in the egg. The former matures and breeds around Lawrance, Kan., during June and early July, and the other during the latter part of August and September.

This question of the true species in *Gryllus* was frequently discussed with my fellow student, Dr. F. E. Lutz, now of Cold Spring Harbor, N. Y., during our study at the University of Chicago. I am glad to confirm his recent publication (*14*) in which he says that the species of *Gryllus* as now named do not differ in characters, "but merely in the degree of common characters." My study has not been especially along the line of taxonomic characters; but my attempts at classifying the specimens collected in Douglas and Harvey counties, Kansas, in Chicago, Ill., in Woods Hole, Mass., in the Santa Rita mountains, Arizona, and in Tarpon, Tex., trying to follow the keys given by Scudder, Blatchley, De Saussure and others, have led me to believe that Lutz is right when he says: "Either we simply name stages in a great continuous mass of variation and call them species or there is but one species of *Gryllus* in eastern United States, and the names we give are not the names of species at all, but simply inaccurate, shorthand expressions for recording the approximate size, proportions and color of individuals found." This applies to our common field crickets; and I do not think that it should be limited to the eastern United States, but should include the central portion as well.

On a collecting trip to Tarpon, Tex., last summer, I found a color variation which confirms this opinion that all these so-called species grade into each other. On the low sandy islands I found that the crickets were *straw yellow*. Most of them were in the last or next to the last nymph stage. This was about June 12. At first I thought they were the imported *Gryllus domesticus;* but later collecting disclosed some with a few, and some with many dark markings. A few of the adults taken subsequently were quite black. These were under the same boards or stones with the straw-colored ones, and were mating with them; and they probably came from the same mother. A number of nymphs were brought to the laboratory at Lawrence and raised to maturity. All of them turned much darker and some became jet black. As far as I could see these black ones could not be distinguished from our native species.

One peculiarity of these crickets on the islands at Tarpon offered an additional reason for thinking they were *G. domesticus*, or a closely allied species; *i. e.*, the young nymphs varied much in their stages of development, a peculiarity I had noticed in the domestic species in the greenhouses in Chicago. This fact must be due to the climatic conditions—both forms developing where there is a long-continued breeding season, with even temperature.

In the laboratory I found that these Texas forms mated very readily with our Kansas forms, both the spring-maturing and autumn-maturing broods. Some of the adults I brought with me paired with some tardy spring forms and some of the smallest nymphs were not matured before autumn adults appeared.

In trying to classify these southern forms I finally concluded that they were our common black field crickets, which had lost *a little, very much,* or *nearly all* of their pigment. Although Blatchley, Scudder, and De Saussure use the color difference as one of the prominent characters separating species, I do not believe that it can properly be so used. "Black color" and "straw color" do not stand for different species in the crickets of the Texas coast. The black gradually shades off into the straw color; and a black one and a light one may have the same mother.

An examination of the germ cells reveals no differences in cell structure between the southern light-colored specimens and our native black ones. But both differ markedly from that found in *Gryllus domesticus,* as has been and will be shown by the papers dealing with spermatogenesis.

All of the collections made in the various localities show dimorphism as to wing length. The short-winged forms are very much more numerous in all places, but the long-winged forms vary greatly in frequency in the several localities, as Lutz (*14*) has found.

Blatchley (*6*) is correct when he suggests that the failure of past monographers of this genus is in part due to the fact that they have neglected the study of the animals in the field. By using this method he has added some very useful hints on the habits and structure, as they bear on the classification. He has plainly shown that there are in many localities really two broods, one maturing early and the other later. He considers them as belonging to different species. Lutz denies this. In whatever region I have observed the two broods, the autumn specimens are larger and more robust than the earlier ones. They also differ in proportions and color enough to represent two species according to ordinary criteria for species; but the intergrading of the forms from different localities would remove all distinctive characteristics. So while Blatchley is apparently right, I feel confident that extensive careful collecting will show that Lutz is correct.

The earlier brood lives "in burrows singly or in pairs," while the later ones "are more sociable," and there is not much "forsaking of burrows," as Blatchley (*6*) thinks. My observations have led me to the following conclusions: Of the spring brood each individual has a separate well-made burrow, early in the season, usually under some stone or board. The male keeps his as long as he lives, or well through the breeding period at least; while the female abandons hers when she becomes an adult, or even before. Thereafter she may be found with the male in his burrow or in any convenient hiding place.

The young individuals of the autumn brood never make much of a burrow, but live under bunches of loose, dry grass or old rags, or whatever they find. I have frequently found more than a dozen in an old newspaper in the grass. The adult males sometimes have a sort of burrow, particularly late in the season, but most of the time I find them in any kind of a hiding place. I am quite sure, however, that these creatures, young and old, especially the males, have a selected spot in the grass or paper, which serves as their home, and so the difference between the spring and autumn forms is really this: the former dig a burrow for a home, while the latter simply select some convenient place to stay.

Judging from my study of the germ cells of *Gryllus domesticus,* given in a former paper (*3*), this species is quite different from the other forms. The difference of chromosome number and shape are such that I should expect the domestic species to be very different in taxonomic characters; but such is not the case.

In other genera of the family Gryllidæ the species are more distinct and limited. In *Œcanthus,* following Hart (*10*), we classify the species largely by the color markings on the basal joints of the antennæ, and this seems to be quite constant. I have found that I can separate the nymphs quite readily by means of these markings. *Nemobius* shows more variation, and probably after large, widespread collecting the species may prove to intergrade. In *Gryllotalpa* the species are quite distinct.

FOOD HABITS.

Very many observers have written of the food habits. It is known that the common black field crickets may eat almost anything. In captivity they will sometimes devour each other, the stronger ones feasting on the weaker ones even before they are dead. I have seen a female chew the wing of a male, and I have found a crippled female with her abdomen partly eaten away. In their free life I think this rarely or never occurs.

The females will eat the empty spermatophores whenever they find them.

Among the mole crickets I observed this peculiarity between two species. In a box of specimens of *Scapteriscus* sent me from Porto Rico I never discovered any partially devoured ones among the few dead specimens; but while collecting our own species *Gryllotalpa borealis,* in northern Indiana, I placed one female adult and six nymphs in a bottle full of sand in the field. When I returned to the laboratory I found but two nymphs, the others having been devoured by the adult. This, with some later experiences, led me to believe that adults will eat the nymphs whenever they find them in their burrowings. However, this cannot be true for the very young nymphs, as the eggs are laid in a mass in a much frequented part of the burrow, and the mother, no doubt, cares for the eggs and young for a while.

EGG-LAYING.

Blatchley (*6*) says: "The eggs of most crickets are laid singly in the ground." My observations confirm this as far as *Gryllus* and *Nemobius* are concerned. The large black field cricket selects usually a somewhat barren spot in a grassy field, where she lays her eggs. She will force her ovipositor into the ground and deposit a single egg, then removing the ovipositor partly will put it down at a different angle and plant another egg, and repeating the process will leave a third. On no occasion did I see more than four eggs laid without the ovipositor being completely removed and pushed into the ground at a new place. *Nemobius* lays its eggs in a similar manner. Two or three, rarely four, eggs are laid almost side by side, and then the next batch are placed a quarter of an inch or more away.

In but one instance did I find eggs laid by the mole cricket. They were "in a heap on the floor in the enlarged part of a side gallery," just as Barrett (*1*) has described.

CHIRPING.

A peculiar habit of the mole crickets, of which I made brief mention in an abstract (*4*), is the *chirping of the female.* A hurried examination of the tegmina of the females will show that the nerves are modified into a rasping and sounding organ, which is not as large or as well developed as that of the male, but well enough to have made thoughtful observers of the past suspect that it might function, and that female *Gryllotalpa* might chirp. As far as I have been able to read the literature no one has observed that they actually do so. Most of our books say that only the males stridulate. LaCordiare (*12*) says, "The chirping organs of the crickets are simple and limited to the males." Scudder, speaking of the crickets, says, "his egotistic love song." Comstock (*7*) writes, "the males of the crickets have musical organs." Lang (*13*) says: "In the Locustidæ and Gryllidæ only the males stridulate, by rubbing the rough basal portions of their wing cases against each other." Packard (*15*), after speaking of the organs in the males, says: "The females are not invariably dumb, both sexes of the European *Ephippigera* being able to faintly stridulate." Henneguy (*11*), in speaking of the musical organs, writes: "Where they are found they are well developed in the males only; in the females they are more or less rudimentary. Such is the case in the Gryllidæ." Barrett (*1*) describes the stridulating organ in the male "Changa" or Porto Rican mole cricket, *Scapteriscus didactylus;* but he has completely overlooked the same but less well developed organ in the female.

The female mole cricket has quite a loud and distinct chirp. It usually consists of a single note; but there may be several at short intervals. This note is less shrill than the ordinary call of the male. However, the male has a note very similar to that of the female which it uses for the same purposes, namely, as a means of recognition in the dark burrows. The call is always given when one individual is approaching another, especially when digging a new tunnel. Both genera, *Gryllotalpa* and *Scapteriscus,* have the stridulating organ on the female elytra, and so both must be able to chirp. I never isolated a Porto Rican female to hear its chirp, but after hearing the call of our native cricket I feel sure that I have heard the insular female's chirp also.

This unusual ability possessed by the female is an adaptation to life in underground burrows. It enables the individuals to recognize others which are approaching under conditions where sight cannot be used. Thus enemies and friends can be distinguished; while if the female were dumb, as she is in all other crickets as far as I know, they might often attack even their mates.

PROTECTIVE GLANDS IN THE MOLE CRICKETS.

As indicated in an abstract (*4*), I have found that the correct interpretation of the function of the anal gland, which has so long puzzled investigators, is protective. Leon Dufour (*8*), a careful French investigator, first described in the mole crickets in both sexes a pair of azure or skim-milk colored glands connected with the rectum. Their secretion he compares in consistency with the vitreous humor of the human eye. To this secretion is added some excrement from the rectum, and when this mixture is expelled it forms a brown liquid of nauseating fetidity. He calls the gland "an organ of excremental secretion."

Berlese (*5*) describes the same structure and thinks it is a prostatic gland analogous to that found in the locustids. Although he found it in the female also, he does not seem to try to explain it there.

Fenard quotes both of the above descriptions and adds a good many observations of his own. He describes the gland from sections and gives the action of certain fixatives and stains upon the tissues of the gland and its contents. He states in detail the macroscopic and microscopic structure. He concludes as follows: "Judging from the position of this organ, from the consistency of the liquid which it contains, and from its points of similarity with the prostatic glands of the locustids, I think that it ought to be considered also as a gland furnishing a mucus destined to lubricate the copulating apparatus. This organ exists in the female, it is true, but in this case it furnishes without doubt still a lubricant for the vagina, or a liquid to form the nest of these insects." After describing the details of this gland in the female he says: "I think that these organs can only be some secreting agent of a mucus destined to lubricate the genital organs; or perhaps they glue together and hold the spermatophores; or perhaps again they secrete the substance used to form the nests in which are found, as we all know, two to three hundred eggs all massed together and more or less united." It is evident from this uncertainty that Fenard did not know the function of the glands in question, yet he was inclined to follow Berlese and called them "prostatic glands."

Packard, in his work on Entomology, places the anal odoriferous glands described by Dufour among the repugnatorial glands, apparently because he has concluded that all fetid and anal glands are repulsive.

As far as the position, size and structure of these glands are concerned, these earlier observers are on the whole correct. They agree, too, in the main points. Dufour has the glands attached to the rectum, while Fenard has them attached to the genital duct. The explanation of this difference of observation is partially suggested by Fenard, when he says: "En somme ces organes paraissent d'eboucher dans une sorte de cloaque ou arrive l'oviducte." The mole crickets have but a single opening at the posterior end of the abdomen; and a short common duct carries the genital and excrementary products. This should very properly be called a "cloaca." Into this cavity the short ducts of the anal glands empty.

Fenard gives as the sizes of the glands "about six millimeters in length and three millimeters in thickness." I found none as large as that, but the size would depend in part upon the amount of secretion in the gland. Both Dufour and Fenard speak of two lobes and a median constriction. There is some tendency for such a constriction to show, but it is not constant. The shape and position of the organ would depend somewhat on the amount of extension of the abdomen and the fullness of the rectum. The two lobes when present do not differ in histological structure, and not in function, as Fenard has shown by his careful work by means of sections. The walls are resistant, the cavity large, and the contents appear homogeneous, granular, and they coagulate as a result of fixation, and color strongly whenever stained. All these facts Fenard has correctly described.

But Fenard must have worked with preserved specimens only, or he would not have made the error concerning the function of the gland. Although he quotes Dufour, he cannot have followed his suggestion when the latter says: "If one seizes a mole cricket of either sex, it squirts from the anus a brown liquid of nauseating fetidity. This liquid is formed in part by excrement from the rectum and is in part the product of a special secretion."

I have studied *Scapteriscus didactylus* from Porto Rico and *Gryllotalpa borealis* taken in northern Indiana and in eastern Kansas. My observations and experiments show that the above quotation is correct in most parts. If the insect is held or irritated in the region of the head or thorax, there is no discharge.

But if held or pinched or pricked or chemically irritated on any side of the posterior part of the abdomen, or on the hind legs, there is always ejected from the anus a bluish-white liquid with some excrement. The discharge is directed as nearly as possible to the point of attack, be it above, below, behind, or on either side of the abdomen. It is driven with considerable force, enough in some instances to carry it across an aquarium eight inches in diameter. After several ejections there is less excrement in the liquid, which becomes almost colorless, losing its milkiness.

The ejected mass has a very fetid odor and is *very sticky,* so sticky that a half-grown nymph can readily be suspended by lightly touching a needle to some of the secretion and then to its abdomen. An adult female, in spite of her strong legs, was held for nearly a minute as a result of touching her besmeared body against the side of the jar.

In some breeding experiments reported elsewhere I was able to study the effect of this ejection and the conditions under which it is made. There was no discharge when the male was carefully introduced into the jar with the female, but on one occasion it happened that the male became excited and rushed upon the female in his attempt to get away. He received a discharge upon his head and into his face. He stood for a long time trying to clean this off. He apparently could remove but little of it, and died on the second day thereafter. At another time a female received a lesser discharge from a male. She, too, spent hours trying to scrape off the sticky stuff, but failed, and died on the third day. The other pair lived for many weeks longer. Perfectly calm individuals, when put into a jar in which there had been a discharge a day or so before, became very much agitated and tried hard to escape from the enclosure. This behavior suggests that when these insects get this odor it warns them that an enemy has been or is near, and they try to escape. I repeated this test several times with the same result. I introduced some affected sand into a jar containing a calm individual. He became agitated. In every instance the crickets became excited when they perceived the odor.

The fetidity of the liquid must repel very ardent pursuers, and the stickiness must retard them should they become entangled in a discharge. It is, no doubt, for the purpose of so entangling the enemy that the cricket directs its discharge toward the point of attack.

This defensive organ probably explains the fact that mole crickets have so few natural enemies, as reported by Barrett (*1*).

Since the Gryllotalpidæ move most of the time in underground burrows the discharge from the anus would protect against attacks from the rear. Hence there is no discharge when the irritation is on the anterior half of the body. The head and thorax, besides being very hard, are further protected by the powerful fore legs. The abdomen is comparatively soft and without other protection than that described above.

My observations and experiments prove conclusively that the secretion of the anal glands, or "prostatic glands" of Berlese and Fenard, is preëminently protective, as any one who will take the trouble to secure a live specimen and repeat these tests can see for himself. Neither Berlese nor Fenard can have handled live individuals, or they should have seen the use of the anal secretion.

As far as we know no other orthopteran has these protective glands, nor has it the same peculiar habits. The mole crickets running along the narrow underground tunnels have the soft abdomens constantly exposed to the attacks of enemies which they cannot see or perceive, so they have developed a special organ which can instantly repel or retard a pursuer.

SUMMARY.

1. The species of *Gryllus* in eastern and central United States are not distinct, but form one large intergrading series, as Lutz has shown. This is true also for the supposed distinguishing *straw* and *dark* colors as shown by the specimens collected in Texas.

2. The female mole cricket has a partially developed chirping organ on its elytra. With this instrument it produces a single note used as means of recognition in the dark tunnels.

3. The anal gland of Dufour, the prostatic gland of Berlese and Fenard, is protective in function. The secretion operates as a repellant by its fetidity, and as a retardant by its stickiness.

4. Both the female musical organ and the protective gland are adaptations to life in underground tunnels.

UNIVERSITY OF KANSAS,
May 10, 1909.

BIBLIOGRAPHY.

1. BARRETT, O. W., 1902. The Changa or Mole Cricket in Porto Rico. Bulletin No. 2, Porto Rico Agricultural Experiment Station.
2. BAUMGARTNER, W. J., 1902. The Spermatid Transformation in *Gryllus assimilis* with Special Reference to the Nebenkern. Kan. Univ. Sci. Bul., vol. 1, No. 1.
3. BAUMGARTNER, W. J., 1904. Some New Evidences for the Indviduality of the Chromosomes. Biol. Bul., vol. VIII, No. 1.
4. BAUMGARTNER, W. J., 1905. Some Peculiar Habits of the Mole Crickets. Science, N. S., vol. XXI, No. 544.
5. BERLESE, A., 1882. Ricerche sugli organi genitali degli Ortotteri. Atti della R. Accad. dei Lincei. Ser. III, vol. XI.
6. BLATCHLEY, W. S., 1902. The Orthoptera of Indiana. Twenty-seventh Annual Report of the Department of Geology and Natural Resources of Indiana.
7. COMSTOCK, J. H. and A. B., 1895. A Manual for the Study of the Insects. Ithaca, N. Y.
8. DUFOUR, LEON, 1841. Recherches anatomiques et physiologiques sur Orthoptères, les Hymènoptères et les Néuroptères. Memoire des Savants étrangers, Paris.
9. FENARD, A., 1897. Recherches sur les organes complémentaires internes de l'appariel génital des Orthoptères. Bull. Sc. France-Belg., vol. XXIX.
10. HART, CHAS. A., 1892. On the Species of Œcanthus. Ent. News, vol. III.
11. HENNEGUY, L. FELIX, 1904. Les Insectes, Morphologie, Reproduction, Embryogénie. Paris.
12. LACORDIARE, M. TH., 1834. Introduction a L' entomologié. Paris.
13. LANG, A. Textbook of Comparative Anatomy. (Translated by H. M. and M. Bernard.) London.
14. LUTZ, F. E., 1908. The Variation and Correlations of Certain Taxonomic Characters of *Gryllus*. Carnegie Institution of Washington, Publication No. 101.
15. PACKARD, A. S., 1893. Textbook of Entomology. London.
16. SAUSSURE, HENRI DE, 1872-'78. Melanges Orthopterologiques. Geneva.
17. SCUDDER, S. H. Notes on the Stridulation of Some New England Orthoptera.
18. SCUDDER, S. H., 1901. The species of *Gryllus* on the Pacific Coast. Psyche, vol. IX.
19. SCUDDER, S. H., 1901. The Species of *Gryllus* Found in the United States East of the Sierra Nevadas. Psyche, vol. IX.

321

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CONTENTS:

OBSERVATIONS ON THE GRYLLIDÆ: IV. COPULATION, *W. J. Baumgartner.*

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OBSERVATIONS ON THE GRYLLIDÆ: IV. COPULATION.

BY W. J. BAUMGARTNER.

(Contribution from the Zoölogical Laboratory, No. 196.)

Plate LXIV.

HISTORICAL NOTE.

THE first suggestion of the correct method of the transfer of the spermatozoa from the male to the female in the Gryllidæ is given by Siebold (*20*), who described the glands annexed to the ejaculatory duct and noted that their secretion coagulated very readily when exposed to the air, and that it probably served to fill and distend the copulatory pouch just as it filled and distended the penis. The latter organ surrounded a portion of the sperm and thus formed the spermatophore. Siebold believed with the older naturalists that the spermatophore is the end of the penis broken off and often reformed.

Stein (*22*) by his careful investigations gave the correct idea of the spermatophore as a vesicle formed by the secretion of the annexed glands and used to carry the sperm. Siebold (*21*) accepted this correction and later defended it. But he studied mostly locustids, and so we do not know that this part of his notes concerned the gryllids; however, some of his work was done on *Gryllus*, and so the work must be mentioned in a review of the subject.

We do have a comparatively detailed description of the act or acts of copulation in the crickets as early as 1855 by a Frenchman, M. Charles Lespes (*11*). But the work was little known and then questioned by Milne-Edwards (*15*); so that textbooks of to-day still disregard it, or quote it with a question mark. Since I shall use Lespes's work very freely in my own description, I shall not review it farther here. Suffice it to say that the observations are strikingly keen and correct for having been made so early, and they should long since have been inserted in our texts.

Leydig (*13*) in his fine work, dealing more with the histological side of the subject, says that in many invertebrates the accessory sex glands form a spermatophore.

Milne-Edwards (*15*), in 1870, said, speaking of the spermatophore mentioned by Stein and Siebold: "It is possible that it may exist in certain cases, but in other cases it is evident to me that the appendage in question was certainly a part of the penis." Of Lespes's statements he writes: "It does not seem to me sufficiently demonstrated that the so-called spermatophore is not the terminal part of the penis which in copulation is broken off and remains inserted in the female apparatus, as it does so often in the case of other insects."

Milne-Edwards's prominent position, no doubt, gave his work the preponderance, and so we find Lespes's work hardly ever quoted. To show how it was disregarded, let me quote from Girard, who wrote three large volumes on entomology. In 1873 (*7*) he said of the glands joined to the *vas deferens*, "They pour in a liquid to delay or modify the sperm." In the third volume, in 1885 (*8*), he repeated the above statement about delaying the sperm, and then adds, "or perhaps to give more activity to the sperm, which are almost immotile in the testis."

Berlese (*4*) studied the external and internal genital organs of various orthopteran species. In the body of his work he does not seem to realize that the Gryllidæ differ from the other Orthoptera, and so he describes in *Gryllus* a penis and all the other accessory parts, without any thought of their correct function. In an appended "Physiological Note" he comes nearer the truth. He says, concerning copulation, that fertilization is internal and that copulation in the Acrididæ and perhaps in the Mantidæ is by means of a penis, the act lasting a relatively long time; while in the Locustidæ and Gryllidæ, "the male mounts on the back of the female, the penis being inserted in the vagina and the sperm injected in a short time."

He supposes that the mucus secretion of the annexed glands serves to lubricate the organs. He notes the fact that in *Gryllus* and *Gryllotalpa* the mucous secretion flows out through the same duct with the sperm. He adds further: "In *Gryllus*, I think, fecundation is more complex, occurring by means of a special organ which is left in the vagina of the female and which can be reformed up to three times a day, as I myself have seen. This singular organ holds the sperm in its interior and is a true spermatophore." The only way I can explain how Berlese came to overlook the discrepancy between his description and his "Physiological Note" is to think that in the body of the paper he was concerned with the homology of the parts in the various groups of Orthoptera, and so did not think of the function.

Graber (*9*) shows that in many Orthoptera there is no true copulation, but that the sperm are transferred by spermatophores. Palmen (*17*) studied by means of dissection and sections several species of Orthoptera, and he confirms Graber, showing the absence of a penis and the correct method of spermatozoon transfer.

Peytoureau (*19*) in his long thesis on the "Morphology of the Genital Armature of Insects," does not even mention Lespes's work, again showing how little this early, accurate investigation is known; or if known, how little it is appreciated. Peytoureau worked on the mole crickets, some long-horned and some short-horned grasshoppers. His special study was the hard parts, and he showed that the penis is absent, except in the Acrididæ, the Forficulidæ and the Ephemeridæ. But his study was centered about the homology of the male and female hard parts. Questions of the number of abdominal segments, the relative position of the ovipositor and the penis and to what segments these belonged, were the ones which he considered; and so the only observation of importance bearing upon our topic is the absence of the penis in the Gryllidæ.

Fenard (*6*) in 1896 published a long paper on "Les Organes Complimentaries Internes de L'appariel Genital des Orthoptères." He studied both sections and dissections of the annexed glands in the two sexes of several genera of most of the families of Orthoptera. In his observations he is correct on the whole. But in his interpretations he is not always so fortunate. The errors made are due largely to the fact, I think, that he worked with preserved specimens only, and so missed the function of parts as proven by the habits of the animals. The suggestion that the anal gland in the mole crickets secretes a lubricant for the genital organs is entirely wrong, as I have shown elsewhere (*2*). Concerning the glands annexed to the ejaculatory duct he reasons correctly, as follows: Gryllids and locustids form a spermatophore, as shown by Siebold (*21*), Lespes (*11*) and Berlese (*4*). But these families are the ones that have this mass of annexed glands; hence these glands secrete the substance for the spermatophore. He thinks there must be a spermatophore formed in *Gryllotalpa,* although it has never been seen because of the habits of these insects. In this surmising he was fortunate, as I show below. But he is mistaken in the function of what he calls the ear-shaped gland. He thinks that it is analogous to the anal gland of *Gryllotalpa.* This is surely wrong. The position of the pair of glands and its relation to the excretory duct is such that it can have no such function as I have found for the anal glands of the mole crickets. My many dissections and observations lead me to believe that there is no gland which secretes a lubricant for the sexual organs.

Although the method of copulation by spermatophore and the function of the annexed glands have been so well described, it is rather disappointing to see our textbooks still quoting Carus's figures showing that the male generative apparatus of *Gryllus* is among the simplest found in the insects. See Henneguy (*10*) *et al.* Although this Frenchman cites Fenard's paper in his bibliography, he makes no reference to his findings, but says of the annexed glands: "Elles ont été peu étudiés jusqu' icé." But under the topic of "Copulation" he gives the process in *Gryllus* in detail, quoting Lespes's description and some of his figures of the spermatophore. In this case he does better than our own Packard (*18*), who, in speaking of the spermatophore, says: "In *Locusta,* and perhaps also in *Gryllus,* the sperm is enveloped by the secretion of the accessory glands of the seminal duct." This "perhaps" is very striking when one considers how easy it is for any one to observe copulation in our common field cricket. One need only catch an individual of each sex during the height of the breeding season, as indicated by their great chorus of chirping, and place them with a little grass over night or longer into separate jars. Then slowly turn the glass with the male over that with the female. In a comparatively short time the male will begin his chirping and one can see the whole series of acts of courting and copulation. After observing the process one can hardly prevent a smile when he reads Loeb's (*14*) quotation of Yersin's experiment of having a pair of decapitated crickets copulate, and then see the admonition: "Of course it was necessary to place the male *on* the female." One would hope that the observations in the experiment itself, and any conclusions drawn therefrom, may be more to the point than is the self-evident suggestion added at the end.

DESCRIPTION.

A free translation of Lespes's paper of 1855 would describe fairly correctly and with a good deal of detail the various steps in the process of copulation. He notes at the beginning that there is no true copulation, but that the male simply deposits a spermatophore into the posterior end of the abdomen of the female; and that this process may be repeated many times.

The Courting.

Lespes (*11*) studied first the field cricket. Catching specimens of both sexes, he got them accustomed to their new surroundings and then brought the two together. "The male soon began to chirp, and to move around the female. Approaching nearer and continuing his chirping he turned his abdomen, carried very low, toward the head of the female. She remained quiet for ten minutes, not appearing to notice the maneuvers of her mate; then she moved forward a little and began to caress his abdomen with her mouth parts. Presently she mounted partly on his back; and he, stopping the chirping, glided back under her. The female vulva now rested above the end of the male abdomen."

This description of the courting is fairly exact. The caressing by the female is not essential or even usual. Sometimes the female hardly stops feeding during the whole process, simply allowing the male to slide under her. When the male approaches the female, or when she approaches him, his chirp becomes much softer and less shrill. On some occasions if the female did not yield after a certain amount of chirping the male became angry and fought his mate.

The Transfer of the Spermatophore.

Lespes says: "The plate, the tenth tergite, which covers the opening of the anus and the pieces of the genital armature, was raised, and a hook of this apparatus penetrated into the vulva. Immediately after this the end of a small brown body directed by the hook was introduced into this opening. The female then left the male, carrying the small brown body of which I have spoken." Lespes then removed the small apparatus from the female quite easily, as only its front end was inserted in the vulva. This apparatus he found composed of a small hard ampulla and a thin, transparent plate curiously twisted. Upon examining a jar in which he kept a male over night he discovered that there was a spermatophore lying on the bottom. He later proved that this was not exceptional, but that males deprived of females rid themselves of their spermatophores.

The male which had copulated with the female seemed exhausted and did not renew his courting for several hours, although he was again put in with the female. Lespes observed the transfer of the spermatophore very often, and each time he got a spermatophore from the female, which he studied later.

Taking up this transfer in detail, the Frenchman describes the position of the spermatophore in the male. "It lies in the posterior end of the abdomen covered by the supra-anal plate. To see it *in situ,* gently raise the anal plate which covers the anus; below this there is a horny plate with three hooks projecting backwards and upwards, and below this there is the spermatophore lying in the concavity of the eighth sternite. The ampulla extends backwards and is supported on either side by fleshy pallets (plate is used by Lespes). The plate and the thread of the apparatus are still in the organs which formed them. At the moment of copulation the supra-anal plate is raised and the hooks are introduced into the vulva, holding the two individuals firmly together. The end of the spermatophore plate from which projects the thread glides in a kind of hollow groove in behind the hook in a manner analogous to that which surgeons use when they introduce a bistoury upon a groove-director. By a rapid movement from before backwards the plate is fastened and the two pallets which hold the ampulla move aside, and so the spermatophore is carried by the female, held by the plate only. Ten minutes after copulation some males had formed a new spermatophore, but it was soft and white, and attained its hardness and color only after an hour. The spermatophore can be quite readily removed from the male by means of a forceps. To form a new spermatophore the male goes through some motions similar to those used in defecation. The female carries the spermatophore for some time, in one case six hours, and it was not dropped until she mounted a male again."

My own observations show that this account is quite correct in most of the details. Our common black field cricket differs in the following points: The female if undisturbed will not leave the male immediately after the placing of the spermatophore. She may remain perfectly quiet for several minutes.

A third element of this sperm-bearer, which Lespes seems to consider of little importance, is very essential, as I shall prove below. It is the thread which projects beyond the plate. (See fig. I.) This thread slides in the groove when the apparatus is being introduced. The mechanical process can be better understood by examining figure 5. The ampulla lies between the two pallets, which are then extended backward very far. The plate lies in the anterior part of the mold and the thread lies in the groove below the hooks. In transferring the spermatophore the male turns the hooks upward by swinging them, or rather the whole mold, at its attachment to the tergite as a pivot. By this turning the hooks first extend upward and then forward and are thus inserted into the vulva of the female, holding her firmly. Then by means of the muscular mass behind, the thread and plate of the spermatophore are pushed far into the vulva. The hooks of the plate hold the apparatus and the thread carries the sperm into the spermatheca. The thread and the anterior end of the plate are quite flexible, and so they are bent and directed by the "independent piece with the short stylet" which guides the thread into the duct leading to the spermatheca. The "forward and backwards" movements are concerned with the proper placing of the thread.

The time suggested for a male to copulate a second time is much too long. I have had a second pairing occur in fifteen minutes. The spermatophore in this case was whiter and softer than usual, but as far as I could see it was a normal copulation. This intervening time was unusually short, but I am sure that it does not take an hour for a spermatophore to harden after it is formed.

I am sure that the males of *our* field crickets rid themselves of the spermatophore, if deprived of the females, only *exceptionally*. In all my many observations I have seen the thing occur but three times, twice in *Gryllus* and once in *Nemobius*. In every case it was rubbed off after an unsuccessful attempt to introduce it into the female. In these trials the plate was, no doubt, partially removed from its normal position in the forming organs, because in most cases the males made no effort to remove the spermatophore, although they had tried to copulate.

I have not seen that the males make any movements while forming a spermatophore, but I would not positively deny that they do so. I have frequently kept them under observation for a few hours after copulation; some would form a new sperm bearer and others not. One male copulated a second time after a very short interval, but I did not watch him meanwhile. Some other specimens did not have the spermatophore formed after hours of watching.

The female carries the vesicle very frequently until she is about to mate again. If this comes soon after a previous copulation, she will remove the vesicle. She does this with her mouth parts, bending the abdomen ventrally. She may place herself partly on her back and holding the abdomen against the ground force her mouth parts back so as to reach the ampulla of the spermatophore. If the abdomen is too much distended by eggs, she frequently rubs it off by dragging the abdomen on the ground. The longer a spermatophore has been carried by the female the easier it is removed. In only one instance did I see a female mount upon a male with the sperm bearer still in place. After a good many efforts the male succeeded in pushing the old spermatophore partially out of the way and placing a new one. The female then carried both, the old one apparently hanging on by one hook.

The Spermatophore.

Lespes says: "The spermatophore of the field cricket is composed of a vesicle almost round, of a brown, more or less dark, color. It terminates at one extremity by a whitish papilla and is continued on the other end by a transparent plate, almost quadrilateral, formed by a thin membrane stretched over three small cartilaginous pieces. One of these is median and connects directly with the vesicle. It is tubular and contains a horny thread which continues well beyond the plate. The other two, situated to the right and left, are arch shaped, and their two ends covered by the membrane, form on either side two tooth-like hooks which serve to fix the apparatus in the vagina. The size of the spermatophore varies a little but ordinarily it attains almost 4 mm. from the papilla to the end of the plate. The thread appears longer or shorter according as it projects more or less from its tube. The spermatophore is of different consistency in different parts. The vesicle is extremely solid and its walls are very thick, while the plate and its cartilaginous thread are soft at the moment of copulation; besides, it is covered by a white, thick liquid which presents to me all the characteristics of a sperm fluid. The thick, hard vesicle, composed apparently of double walls, toward the extremities is hollowed out at the center. The roundish cavity is full of sperm. At one end a blind tube projects from the cavity into the ampulla. At the other end the cavity continues as a straight canal through the whole length of the plate. This canal contains the horny thread.

"The white liquid which covers the plate when first removed from the female shows, when examined with a high magnifier, a large number of small, thread-like zoösperms. They are about .04 mm. long and .002 mm. thick. These same bodies in great number fill the cavity of the vesicle. They were never united into feather-like bundles, nor did they ever show any movement. The fluid taken from the testis of the male or the copulating pouch of the female contains many very similar zoösperms. These never exhibited movement, however treated. Put into water, some of them twisted themselves into knots.

"When the female lets the spermatophore fall the walls of the vesicle are slightly ridged, but it still contains some sperm. The horny thread is no longer found in the tube of the plate."

I have quoted the above description at length because it gives many facts as I find them in our American species.

The vesicle and the plate are similar to those described above (see figs. 1 and 2). The thread is not contained in the tube, but it is the tube itself continued, and it is much longer, and bent back so as to run parallel with the plane of the plate and vesicle (see fig. 1). It is a hollow tube for its whole length and the sperm comes out at the *end* of the thread, and not at the end of the plate, as Lespes supposed. The thread varies in length not because "it projects more or less from the tube" but because it is broken off in removing it from the insect. Many of those that I secured at first had more or less of the end broken off. It is easier to get a spermatophore with a complete thread from the male than from the female, especially if the latter has carried the apparatus for some time. This no doubt accounts for the fact that the apparatus can be more easily removed after it has been carried for a while. When the insect drops it normally the thread has been broken off, or, more probably, partly dissolved away; but it is not entirely gone, as Lespes states.

The vesicle is apparently double-walled as the Frenchman observes (figs. 1, 2, and 3). The inner one is thicker and more granular, while the outer one is harder and quite transparent (figs. 1 and 2). It is the inner wall that continues forward and forms the thread, although this substance is less granular than that around the vesicle. The substance forming the plate is somewhat granular, and in some cases took the stain just like the inner coat of the vesicle. In the lateral parts of the plates I saw in several of my preparations many vacuoles. The thread in many of the specimens fixed and mounted in balsam shows a tendency to break away from the plate (fig. 3).

That the sperm pass out at the end of the thread was nicely shown by several specimens which I placed into a normal salt solution. The sperm flowed out very regularly and moved about for a time. In one instance it took about fifteen minutes for a vesicle to empty itself through the end of the thread. After the sperm were all out a little fluid with small granules flowed out. I do not agree with Lespes when he says that some sperm remain in the vesicle normally; nor do I think that the wrinkling is a characteristic of the empty vesicle. I could not see any difference between an empty spermatophore and a dark brown one which had been carried by a male for some time. The wrinkling, which Lespes correctly describes, is due to the longer hardening of the vesicle and does not seem to affect the cavity on the inside.

The shape of the cavity differs from that described and figured by Lespes in the total absence of the blind tube extending into the papilla. What he describes is only the second layer of the wall of the vesicle as shown in figures 1 to 3. The dark stain here shows the outer limits of the inner lining, and the cavity is on the inside, as shown in the outline drawings. The cavity is easily visible in the preparations but the photos do not bring it out. At the posterior end the cavity is flattened and at the other end it gradually tapers down to the size of the thread; so that the shape of the opening is much like a flat-bottomed flask. In this cavity all the sperm have their heads directed toward the openings into the thread and their tails toward the papilla. Figure 11 is a small group of sperm photographed from a section of a spermatophore. In passing out of the thread the sperm manifested some movement of their own, but were not very active. Several may pass out together but only two or three heads have room side by side. The sperm are larger than Lespes thought, as can be seen by comparing with my earlier published measurements (*1*).

The Spermatophore-forming Organ.

Since many of our textbooks on entomology—see Packard (*18*) and Henneguy (*10*)—still cite *Gryllus* as showing one of the simpler conditions for the excreting ducts of the testes among the insects, I shall give a more detailed account of the male generative organs, their ducts and the accessory glands, than I should otherwise do.

The first description of these parts was given by Dufour (*5*), in *Gryllus campestris*, then by Lespes (*11*), in *G. domesticus*, later by Berlese (*4*), again in *G. campestris*, and then by Fenard (*6*), in both of the above species.

The testes lie on either side of the abdomen above the alimentary canal and extend from the second to the sixth or seventh segments. The shape is much like that of an elongated strawberry. On the outside is a thin membrane which encloses the hundreds of straight or slightly curved tubules which make up the organ (figs. 6 and 7). Their blind ends are nearly all directed more toward the posterior end of the body of the animal. At the center of the testes is a large tube, or rather an irregular sinus, which receives the openings of the hundreds of tubules (fig. 8). The small *vas deferens* leaves this sinus on the anterior ventral side and comes to the ventral side of the testes a little back of the middle. It passes backward over the tubules, and leaving them at the outer posterior edge passes back along the body wall muscles till it reaches the ninth segment, where it passes around the cercal nerve and a few strands of muscle and ligament (figs. 7 and 8). Making a sharp bend it goes forward and ventralward. It is very much coiled upon itself from the bend on (figs. 7 and 8). The loops of the coils may lie in planes passing dorso-ventrally or laterally. The two *vasa deferentia* join and immediately empty into the posterior ventral angle of the sinus, which receives the openings of the annexed glands (fig. 9). Beginning at the cercal nerve and sometimes a little in front of the bend the duct is swollen so as to be 0.5 to 0.75 mm. in diameter (figs. 7 and 8). Fenard says there are from four to five coils and that the total length is 8 mm. In our common field cricket I found no regularity about the position or number of coils and the total length is more than 10 mm.

This swollen part of the *vas deferens* is always in the mature adult filled with a mass of sperm, all of them with their heads turned away from the testis.

Fenard (*6*), as well as the older investigators, says that "the union of the two *vasa deferentia* forms the ejaculatory duct." This is the statement generally made of the insects higher in the scale of evolution; but it is true only in a certain sense—in the sense that it serves as a common duct to carry out the secretions of the testes. First, it is not a true ejaculatory duct in the sense that it "during coition conducts the sperm into the copulatory pouch of the female"—Packard (*18*). This is true only in those insects with a penis; but in the Gryllidæ, where there is a spermatophore formed there can be no such function. Second, nor is it true in the sense that it is formed by a growing together of the two *vasa deferentia*. It is formed by an invagination from the outside, as was first shown by Palmen (*17*) from the anatomical standpoint and by Nusbaum (*16*) from the embryological. This invagination projects quite far beyond the point at which the two *vasa deferentia* join it (fig. 7). It extends dorsalward and forward, where it receives the openings of the hundreds and hundreds of tubules of the annexed glands (fig. 9). The lumen is very much flattened laterally and widened vertically towards the blind end. The more muscular tube leaves the sinus at the posterior dorsal angle just above the point of entrance of the *vasa*. This is well shown in figure 9. The openings of the *vasa* cannot be recognized in this figure, but the serial sections leave no doubt as to its location.

The hundreds of glandular tubules which empty into the upper end of the common duct vary greatly in length and diameter, apparently depending in part upon the room they find for development (figs. 6, 7 and 9). They take up all the available space, completely surrounding the seminal vesicles, extending far backward beside the rectum and the spermatophore pouch, or crowding forward and upward around the intestinal tract. Many of them are short while others are long. The whole group of tubules forms a large mass which takes up quite a space (fig. 6).

The "prostatic gland," first noticed by Berlese and later described by Fenard, I found "only after much difficulty," as the latter says. From my dissections I had concluded that the part so described was a part of the irregular pouch which molds the plate of the spermatophore. But a careful study of serial sections reveals the presence of a pair of oval glands or pockets attached on either side to the common duct. They have very short connecting tubes and they lie in the muscular and connective tissue surrounding that part of the common duct between the ganglion and the mold. The glands are not surrounded by "yellowish fat," as Fenard suggested; but they have "thin walls and are filled with a clear fluid." This fluid seems to harden into a clear yellowish chitin-like substance when treated with fixatives. In this it resembles the secretion from the annexed glands; but their secretion is darker and more granular. Judging from the behavior of the secretion and the position and connections of these glands I think they do not furnish a lubricant, but probably have something to do with the formation of the more flexible thread and the plate.

The common duct, after passing close to the floor of the abdomen, turns dorsalward and then empties into the cavity of the spermatophore mold (fig. 9). This apparatus was carefully studied by Lespes (*11*). Many of his observations are keen and to the point, but his description in some points is not very clear. Berlese (*4*) studied this structure too, but he could not get away from the idea that he was dealing with the ordinary structures, so he applies the name "penis," etc., to the parts and so makes his description misleading. Fenard (*6*) pays no attention to the hard structures and so he does not make out the relations and functions of parts in this region. Peytoureau (*19*) studied mostly only the morphological relations of the hard parts and so he does not explain the functions of the parts of this organ.

Lespes describes this apparatus "charged with the formation of the spermatophore" as follows:

"It is situated at the posterior part of the ejaculatory duct and may be considered as a part of the genital armature. In the field cricket this armature is formed, first, by a curved plate composed of many pieces extending to the right and left and united by a tough membrane; and second, by a very remarkable independent inferior part. The plate itself is composed of six solid pieces. Above is a kind of shield-like piece which is easily divided along the median line. Posteriorly it ends in three hooks, of which the middle one plays an important part in copulation. To the right and left are long slender rods upon which are inserted the fleshy pallets which support the vesicle of the spermatophore. Below this shield are two others, thin and curved, with an irregular contour. Finally, on the inferior face of the dorsal shield are two small, slender plates. During copulation the median hook only enters the vagina and serves to conduct the plate of the spermatophore. The independent piece is formed in front by a sort of short stylet which is applied to the inferior face of the plate of which I have just spoken. At the base this stylet enlarges, changes its nature and forms a white plate with cross striations. This plate is bent along its length, forming an irregular circle. It is swollen into a very thin vesicle situated under the genital armature and in front of the two pallets which support the ampulla of the spermatophore. This pocket is largely open in front and under the genital armature. The ejaculatory duct, after having passed around the lower part of the spermatophore pouch, ends near this opening.

"This white plate is the organ for the production of the spermatophore. On its convex surface is a transparent line in which is formed the tube which holds the thread of the spermatophore. The size of the plate is greater at the two ends. At the terminal part of the enlarged inferior portion ends the ejaculatory duct."

Lespes claims to have seen the spermatophore while it was forming. "It had a very thin membrane. When completely formed the vesicle was removed out to the place between the two fleshy pallets, and the plate and the thread remained in the forming organ, that is, in the stylet of the armature, until given off to the female."

This description is somewhat indefinite because of the uncertain meaning of the phrase "genital armature." Besides, the application of the words "in front" and "behind" is not certain. I do not believe that the differences between Lespes's description and my observations can be accounted for by supposing such differences exist in the different species studied. Both of us used *Gryllus domesticus* some, and as shown below we found only small minor differences between the house cricket and our own species of field crickets.

Before discussing the formation of this peculiar spermatophore farther let me state as clearly as possible the mechanical problem involved. There is a mold made up of a system of bracing rods of chitinous material and a thin fibro-muscular membrane. Into this mold leads a single tube, which has to bring the sperm and the secreted fluid for the covering. The ampullar part of the finished spermatophore has apparently a double wall, and so there may possibly be two kinds of secretions, although a careful study of the gland shown in figure 10 makes me doubt it. The question is, then: How are the sperm kept separate, and especially how are they *held* in the center while the soft liquid is poured around them and hardens? If there is a second layer in the wall the incomplete ampulla would have to be held in the center while the second inflow and hardening occurs. To place a semifluid substance within another fluid substance and hold the former at the center while the latter hardens would be a difficult feat for any mechanic. I do not see how the apparatus provided is sufficient to accomplish the result. Yet I have seen so many well-formed spermatophores that there can be no doubt of the end product.

The way to solve the problem readily suggests itself. One needs to get a lot of specimens showing the various stages in the formation of the vesicle. Such a series of stages I have been hoping to get, but have thus far not succeeded. In all my many dissections I have never found a partially formed vesicle. It is hardly feasible to follow the process in a living specimen, as the attempts to make observations would interfere with the normal formation.

Although I am not able to give a description of the exact method of formation, I shall nevertheless make some suggestions. Lespes says that the ampulla is formed and then moved out to its position between the two pallets. I think that this cannot be correct, as it would mean that the plate and thread would have to be joined onto the ampulla. In all the specimens I have seen the inside cavity and the walls are just as smooth as they can be. I cannot imagine that if the apparatus is formed in two parts they could be joined together so exactly and smoothly. I would rather believe that the structure is formed as a whole *in situ.* The thing that gave the idea that it moved back is the fact that when the wall has partly hardened the pallets retract a little, exposing the ampulla.

When there is no spermatophore in a male cricket the hooks are drawn far down, the pallets are much contracted and folded, and a part of the loose tissue on the floor of the cavity is rolled up and fits into the mold as a sort of plug. The pallets and the plug have deeply grooved and ridged surfaces which line the small lumen within.

Things occur about as follows when a spermatophore is formed: The inner lumen becomes a little larger and assumes the shape of the cavity of the vesicle. Then the sperm pass down, filling it up. It is possible that the lining cells secrete a small amount of substance to form a thin membrane, and Lespes may have found an example in this stage. If a membrane is secreted it cannot be discerned later. Now some secretion comes down the common duct. This flows in and fills up the grooves. The ridges withdraw, forming new grooves to be filled up. The process continues till enough is laid down to form the inner layer of the wall. Then the flow ceases for a while, and the secretion hardens somewhat. After a longer or shorter time a second inflow of secretion occurs, and it takes the place of the withdrawn ridges till the surface of the lining membrane becomes smooth, thus forming the outer wall of the ampulla. Then the whole hardens into the completed spermatophore. I think the whole takes place in a short time relatively. There may be movements accompanying the process, although I have not observed them.

Since there is but one duct, the only other assumption which could be made is that the secretion and the sperm come down all together instead of in succession. If this be correct, then the long sperm would have to wiggle their way to the center. This is hardly possible. Besides, it would be difficult to explain the second layer in the wall of the ampulla by this hypothesis.

Another mechanical problem appears in the study of the spermatophore, namely, What causes the sperm fluid to flow out of the ampulla? Are they forced by contraction of the walls, or is there some substance that swells and forces them out? Does air penetrate the wall in some way and thus prevent a vacuum?

I do not believe that there is any contraction; at least not much. The walls do not collapse. Farther than this I could find nothing that would throw any light on the problem.

Differences Found in the Domestic Cricket.

Lespes describes the spermatophore and the spermatophore-forming organ of this species, but says that he has not seen the act of copulation. I can readily believe the latter statement, as the insects are much more shy and will not mate readily when watched. Nevertheless I witnessed the process several times. The behavior during courting and the movements during the transfer of the spermatophore are very similar to those of the field crickets. The differences are of no consequence.

The spermatophore is lighter in color, as Lespes says. But this is in accord with the general lack of color in this species. It is a little shorter and stouter, as the Frenchman indicated. The plate is also narrower and more bent. But the cavity does not extend back into the papilla, as I have already explained about our field crickets.

There is one point to which I should like to call attention. Lespes does not speak of it, yet shows a difference in the drawings. In the house cricket the thread is a direct continuation of the canal. This is correct for this species, and is precisely what I find in our field cricket. I have not seen the spermatophore in *G. campestris;* but judging from our domestic and field crickets, and the conditions I find in *Nemobius*, I do not believe that Lespes is correct when he indicates a break between the thread and the plate, as he shows in his drawings, figure 2. The canal could not be continuous if his drawing is correct. But Lespes thought that the thread was the mass of sperm, and so not thinking of the thread as a hollow conducting tube he might have a break in it.

The mold differs from that of our field cricket about as it differs from *Gryllus campestris*, judging from Lespes's description. The hooks on the superior plate are rudimentary or absent, while the stylet is well developed and projects far backward. The cavity is smaller, making it necessary that the plate of the spermatophore be bent into a smaller curve. There are other minor differences in size and relations. Whether these differences are great enough to prevent intercrossing of species is not positively settled. I tried some experiments in cross-breeding, in which I was unable to get any cross matings; but the tests were not extensive enough to be very conclusive.

IN NEMOBIUS.

This genus resembles rather closely the form which Lespes describes under the name *Gryllus Sylvestris.* It is much smaller than our *Gryllus* and, like the European form, it likes the woods or shady places; in the grass under the trees of a park I have found the most specimens. In the months of August and September they are very numerous.

In its courting it is, like the domestic cricket, much more shy than the larger form, and it is rather tedious to watch till one catches a pair copulating. In the main the whole series of processes is quite similar to that in *Gryllus.* In the courting the male is more active while the female less readily yields to the courting. What Lespes (*12*) says of his forms holds true for our two genera: "Except some details of form and size all is similar. The spermatophore is smaller and more fragile but is similarly composed. The genital armature presents the same pieces, but they differ much in form." Lespes again in this species figures and describes the thread as continuous with the canal of the plate. This strengthens my belief that there is some mistake in the description of the spermatophore of *Gryllus campestris.*

I have succeeded in getting a good photograph (fig. 4), that shows the structure of the spermatophore of *Nemobius fasciatus,* our most common species, very well. The ampulla is almost a perfect sphere. Its wall is thick and its central cavity rather small and nearly spherical. As in *Gryllus sylvestris,* the plate is small and far from the ampulla, but the thread and plate are much more curved in our species (fig. 4). There is a fine, hollow, tube-like opening leading from the central cavity to the tip of the thread. There can be no doubt that the sperm fluid flows out through it.

IN GRYLLOTALPA.

Fenard (*6*) cites the fact that the Locustidæ and the Gryllidæ produce spermatophores and that those two families have the large mass of annexed glands. Continuing, he says: "Then wherever we find the glandular tubes similar to those in the above-mentioned groups we have a right to conclude, until there is proof to the contrary, that they secrete a substance destined for the formation of spermatophores more or less complex." He suggests that in *Gryllotalpa*, whose copulation has never been seen, fertilization occurs by means of a spermatophore, because they have the annexed glands similar to those of *Gryllus*.

In the abstract (*2*) I made the statement that in the mole crickets the sperm are transferred by means of a spermatophore. In order to observe copulation I kept four mole crickets, two pairs, for several weeks each in a separate aquarium partly filled with wet sand, grass roots and slices of potatoes. For five nights I placed them by pairs into battery jars which contained just enough sand to allow the animals to make a burrow around the edge. Thus I could watch them continuously. After some twenty hours I finally observed copulation. As a result of these vigils I am able to give the facts concerning chirping and the protective gland published elsewhere (*3*), as well as the following concerning copulation.

The courting is somewhat similar to that in *Gryllus*. The male calls the female with loud, long chirps. As she approaches the chirps become short and much softer. He then frequently turns his abdomen towards her. As the pair get ready to copulate the position assumed is quite different from that of any other animals of which I know. They turn posterior end to posterior end, and ventral side to ventral side, so that the cloacal openings are just opposite each other. The female stands erect with her abdomen slightly raised, while the male lies on his back. The abdomens are tightly held together by hooks, described with great detail by Peytoureau (*19*). The sperm were carried to the female by a spermatophore. The time it takes for the transfer is not over a minute; but the pair kept their relative position, the abdomens simply touching each other, for more than ten minutes. After disturbance the male followed the female and again assumed this relative position, but no further transfer of a spermatophore occurred.

Right after the first separation of the couple the female began to chew at a part of the sperm vesicle, and only desisted when disturbed by the movements of the male. She was also perfectly quiet as soon as her abdomen was touched as in the position of copulation. One observation is not enough to establish the purpose of an act; yet, judging from the behavior of the individuals of this pair, especially from the anxiety of the male to touch the female with his abdomen, one could easily conclude that the long lying in the position of copulation was to prevent the female from chewing at the spermatophore too soon and thus preventing the proper injection of the sperm. After the pair had remained in the above-described position for ten minutes or more the female left the male and manifested no further desire to chew the spermatophore. She carried it for about a half an hour and then dropped it.

As the vesicle was being transferred, or just after it had been put in place, there was an outflow of some transparent fluid on either side of the vesicle. This soon hardened. It is this part of the apparatus that the female was chewing. The spermatophore was found to consist of an oval ampulla which contained the sperm in the cavity at the center. At one end of the ampulla there is a projection by which the apparatus is held in the vagina, and through which the sperm are carried into the spermatheca. On either side of this projection is an irregularly shaped mass formed by the above-mentioned outflowing fluid during the transfer. The two sides are unlike, as part of one side was pulled and eaten away by the female, and the other side was pressed out of shape by some falling sand before it had time to harden. Having but this one imperfect specimen of the spermatophore of these crickets I cannot give as accurate a description of its detail as I should like. Suffice it to say that it has the essential parts—a hollow ampulla to contain the sperm and a projecting part to fasten it to the female and to carry in the sperm. The structure of the latter is obscured by the irregular mass.

The outflow of this fluid recalls an observation which I made repeatedly in the Chicago greenhouses. In the copulation of a locustid the same phenomenon occurs, but in a more marked way. The species, an exotic one introduced from Japan, is very abundant in the greenhouses. The male has no chirping organs and so the courting is all done by means of the long antennæ. The female mounts on the back of the male, when he hooks an almost spherical ampulla full of sperm into her vagina. During the latter act a viscid fluid flows out on either side and forms two somewhat irregular roundish masses larger than the original ampulla, which now lies between the two. Sometimes the female began immediately after copulation to eat this substance, doing it more readily if the couple was disturbed.

As to a use or meaning for this outflow of fluid and its subsequent hardening it is difficult to suggest a satisfactory one. Of its regular occurrence there can be no doubt, as I observed it many times in *Diastremmena* and once in *Gryllotalpa.* It may function as an additional fastener to hold the apparatus in the vagina. Yet this seems hardly necessary, as the spermatophore apparently remains in place before it is hardened. It may have something to do with the emptying of the vesicle, contracting around the ampulla, thus forcing out the sperm. Or it may be concerned with the removal of the spermatophore from the vagina, acting as a bait for the female to remove it.

SUMMARY.

1. The reproductive apparatus of *Gryllus* is not of the simplest type, as was reported by the earlier investigators and as is still suggested by our textbooks. These organs are rather of the most complex kind found among the insects. They were studied and described with a good deal of detail, and the correct method of the transfer of the spermatozoa was indicated by Lespes in 1855; but the work was discredited and neglected.
2. The male carries the sperm to the female in a special structure, the spermatophore, formed by the secretion of the glands annexed to the common duct.
3. The essentials of the spermatophore, as shown by the study of several genera of Gryllidæ, are a hollow vesicle to act as a retainer, and a hollow thread-like tube which carries the sperm into the spermatheca of the female. To the tube are added some enlargements which serve to hold the structure in the vagina.
4. The so-called genital armature of the male crickets consists of a mold for forming the spermatophore and an apparatus to transfer the same to the female.

5. The differences between the field and domestic crickets is probably great enough to prevent intermating, yet this is not at all proven.

6. *Gryllus* has no gland which secretes a lubricant for the copulatory organs. The so-called "prostatic gland" has to do with the formation of the thread and plate of the spermatophore.

7. Mole crickets form a spermatophore. A transparent viscid fluid flows out during the transfer. The male and the female assume a very peculiar position relative to one another during copulation.

University of Kansas,
March 12, 1910.

BIBLIOGRAPHY.

1. Baumgartner, W. J., 1902. Spermatid Transformations in *Gryllus assimilis*. Kan. Univ. Sci. Bull., vol. I, No. 2.
2. Baumgartner, W. J., 1905. Observations on Some Peculiar Habits of the Mole Crickets. (Abstract.) Science, N. S., vol. XXI, No. 544.
3. Baumgartner, W. J., 1910. Observations on the Gryllidæ; III. Notes on the Classification and Some Habits of the Crickets. Kan. Univ. Sci. Bull., vol. V, No. 18.
4. Berlese, Antonia, 1882. Ricerche sugli organi genitali degli Ortotterri. Atti della Accademia dei Lincei, 1882.
5. Dufour, Leon, 1841. Recherches anatomiques et physiologiques sur les Orthoptères, les Hymenoptères et les Neuroptères. Mem. d. Savants etrangers, VII, Paris.
6. Fenard, A., 1896. Recherches sur les organes complementaires internes de l'appareil genital des Orthoptères. Theses presentees a la Faculte des Sciences de Paris. Lille.
7. Girard, Maurice, 1873. Traite elementaire d'entomologie, vol. I, Librairie J. B. Baillere et fils, Paris.
8. Girard, Maurice, 1885. Traite elementairie d'entomologie, vol. III, Librairie J. B. Baillere et fils, Paris.
9. Graber, 1877-'79. Die Insecten, vol. I-II, München.
10. Henneguy, L. F., 1904. Les Insectes, Masson et Cie, Paris.
11. Lespes, Chas., 1855. Memoire sur les Spermatophores des Grillons. Ann. Sc. Nat., T. III.
12. Lespes, Chas., 1855. Deuxieme Note sur les Spermatophores du *Gryllus sylvestris*. Ann. Sc. Nat., T. IV.
13. Leydig, Franz, 1867. Der Eierstock und die Samentasche der Insekten, zugleich einen Beitrag zur Lehre der Befruchtung. Nova Acta Acad. Leop. Car., T. XXXIII, Dresden.
14. Loeb, J., 1907. Comparative Physiology of the Brain and Comparative Psychology, New York.
15. Milne-Edwards, H., 1870. Lecons sur la Physiologie et Anatomie comparee de l'homme et des animaux, T. IX.

16. **Nusbaum**, 1882. Zur Entwickelungsgeschichte der Ausführungsgänge der sexualdrüsen bei den Insecten. Zool. Anz., Bd. V.
17. **Palmen**, J. A., 1884. Uber paarige Ausführungsgänge des geschlechtsorgane bei den Insekten. Eine morphologische Untersuchung. Helsingfors.
18. **Packard**, A. S., 1903. A Textbook of Entomology. The Macmillan Company, New York.
19. **Peytoureau**, A., 1895. Morphologie de l'Armure des Insectes, Paris.
20. **Siebold**, C. T., 1837. Fernere Beobachtungen über die Spermatozoen bei wirbellosen Thieren. Mueller's Archiv.
21. **Siebold**, C. T., 1845. Uber die Spermatozoiden der Locustinen. Nova Acta Acad., T. XXI.
22. **Stein**, F., 1847. Vergleichende Anatomie und Physiologie der Insection. I. Die Weiblichen Geschlechtsorgane der Käfer, Berlin.

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CONTENTS:

AN EXAMINATION OF THE CHROMOSOMES OF ANASA TRISTIS:
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AN EXAMINATION OF THE CHROMOSOMES OF ANASA TRISTIS.

BY C. E. M'CLUNG AND EDITH PINNEY.

I. Introductory statement.
II. The chromosomes during the spermatogenesis of Anasa, an independent study: By the junior author.
III. A comparison of the results of studies upon the chromosomes of Anasa: By the senior author.
  1. Methods.
  2. What is the number of spermatogonial chromosomes, and of oögonial chromosomes?
  3. What is the number of first spermatocyte chromosomes?
  4. What is the behavior of the accessory chromosome and of the plasmasome in the first spermatocyte prophase?
  5. What is the behavior of the accessory chromosome in the first spermatocyte mitosis?
  6. What is the behavior of the chromosomes in interkinesis?
  7. What is the behavior of the accessory chromosome in the second spermatocyte mitosis?
  8. What is the final chromosome constitution of the spermatozoa?

I. INTRODUCTORY STATEMENT.

The extensive studies now in progress upon the chromosomes of numerous species of plants and animals have led to the formulation of several working hypotheses of considerable general importance. In order that these may be of value and serve as an aid to further progress, it is necessary that the phenomena from which they take their origin be extensively recognized and uniformly interpreted. Any conception of the relations existing between germ-cell organization, as exhibited by the chromosomes, and the structural characters of the body is now unfortunately delayed by certain disagreements upon the actuality of the phenomena upon which such interpretations are based.

Fundamentally, these disagreements concern more or less intimately that view of chromosome organization which is called the "theory of chromosome individuality." Modern cytologists are either supporters or opponents of this theory, and its adequacy or inadequacy will be determined by the weight of evidence now accumulating. It is, of course, impossible to conceive that it will stand unmodified, for it is but the expression of our present limited knowledge; but it must now be determined whether these structures of the cell have persistent individualities or whether they are merely incidental and inconstant expressions of more fundamental phenomena. Observed facts must support one or the other of these alternatives, although in doing so they may readily enough modify the established order.

A considerable body of evidence has accumulated within recent years to support the theory of chromosome individuality and to associate the development of sexual characters with particular chromosomes. To this has been added the support of experimental work on sex determination and the parallelism between the segregation of Mendelian characters and the behavior of the chromosomes in the maturation divisions of the germ cells. Much of this cytological work has been done upon the insects, particularly in the orders Orthoptera and Hemiptera, and, in the large, there is a strong consensus of opinion. More recently confirmatory evidence has been furnished from studies upon nematodes, including Ascaris, by Boveri, upon echinoderms by Baltzer, and upon birds and man by Guyer. Here and there, however, there are workers who question the fundamental facts and deny the correctness of the theories founded upon them.

It is necessary, in order to proceed further with our interpretations, that we reach an agreement upon the observable facts in our science, and no honest question should remain without answer.

At present one of the most serious diversities of opinion exists regarding the character and the behavior of the accessory chromosome in the bug *Anasa tristis.* Because of the extensive and painstaking studies of hemipteran germ cells by Wilson, the contradictions and inaccuracies in the studies of

Paulmier and of Montgomery seemed to be cleared up and the phenomena in this order brought into agreement with those of the other insects. To this was added the confirmatory work of Stevens upon several orders of insects, the study of Lefevre and McGill on *Anasa*, and more recently that of Morgan on aphids and phylloxerans. Directly opposed to all this are the observations of Foot and Strobell upon *Anasa tristis*, the form studied in detail by Paulmier, Montgomery and Wilson. Their contention, in brief, is that the number of spermatogonial chromosomes is even instead of odd, that there is no dimorphism of the spermatozoa due to the presence in one-half their number of the accessory chromosome, and that there is no evidence to show that the theory of chromosome individuality receives any support from observed morphological continuity of any of the chromosomes. Aside from these major questions there are others, such as the history and fate of the plasmasome, upon which these authors are in disagreement with other investigators.

The issues here defined are so clear-cut and definite and their settlement of so much importance that the senior author of the present paper was led to offer his services for a reëxamination of the whole question. This offer met a hearty response from Professor Wilson, who sent not only live material, but his entire series of mounted slides, including those used by Paulmier. Professor Lefevre has been kind enough, also, to permit the use of his slides. Miss Strobell, writing for Miss Foot, expressed a lively interest in the proposed settlement of this problem, but was unable to send the preparations used in their studies, because these had all been destroyed on account of limited storage room. It is to be regretted that this material is not available for comparison, since it is upon it that the only divergent observations have been made; but since specimens from the same locality, prepared by all methods, including the special ones employed by the Misses Foot and Strobell, are at hand, there can be no reasonable doubt that it is representative.

To reduce the possibility of the influence of preconception to the lowest possible degree, the junior author has worked through the entire problem without knowledge of the work done by others, and without promptings from the senior author except such as were given by a series of questions for which answers were desired. Independently, the senior author went over the same ground, first upon material prepared in this laboratory, and later upon the slides of Paulmier, Wilson and Lefevre. Whenever possible, photomicrographs were made, and representations of them accompany the paper. The two authors reached concordant results throughout, and their common experience is embodied in what follows.

Since the matters of dispute are purely of facts and interpretations, it will be necessary to take a definite position on each of the points involved, but so far as possible the material evidence for the decisions will be presented fully. It is hoped that this may be complete enough so that others interested may be able to form their own opinions directly from the appearances themselves. There will be presented first the personal work of the junior author, giving her independent results, and this will be followed by a general discussion of the problem by the senior author.

II. THE CHROMOSOMES DURING THE SPERMATOGENESIS OF ANASA TRISTIS.

BY EDITH PINNEY.

Preparatory to an attempted settlement of various disputed questions in the development of the germ cells of *Anasa tristis* an independent reëxamination of the entire process was undertaken. In order to avoid unconscious bias of opinion the previous reports on the spermatogenesis of this species were not read. Without referring, therefore, to the accounts of other observers for comparison or correlation it is purposed to record the results of these observations.

Material.—Preparation and general description.

Material was taken from specimens of *Anasa* collected in Lawrence, Kan., and in Woods Hole, Mass. The latter was obtained through the courtesy of Dr. E. B. Wilson, of Columbia University. All material was fixed in Flemming's fluid, the period of fixation varying from one-half to two hours. The longer fixation was found to give the better results. Paraffin sections were cut five micra in thickness and stained by Heidenhain's iron-hæmatoxylin, Flemming's tricolor and Auerbach's methods. Slides prepared by the author from nineteen individuals were studied. Most of the drawings were made at a magnification of 3625 diameters. This is reduced one-half in reproduction.

The testes of *Anasa tristis* are paired organs in the form of two small fig-shaped bodies which lie on either side of the median line in the cephalo-ventral part of the abdominal cavity. They are composed of a number of long, slender follicles lying parallel to each other and extending the entire length of the testis. The follicles themselves taper slightly from the broader base toward the sperm-duct. The follicular organization into cysts of germ cells of varying stages of maturation is similar to that in the Orthoptera, and the same method which was used to determine the sequence of the observed changes in the Orthopteran species is applicable here. Practically all of the cells of a cyst are in the same phase, although exceptions to this regularity are frequent in the older cysts, particularly those of the first and second spermatocyte generations. These variations are, however, to be expected, and may reasonably be accounted for if one considers the unavoidable differences which must occur in the rate of metabolism in cells situated differently in the same cyst.

The longitudinal section of a follicle presents some noticeable features of a structural nature caused by characteristic differences in the cells of various regions. The spermatogonial cells occupy the distal portion of the follicle, the extent of the spermatogonial area being determined by the age of the individual. These cells are small, and in the older cysts the nucleus is accompanied by little cytoplasm. Hence the peculiar staining quality of the nuclear material causes this region to appear more intensely stained than the proximal portion of the follicle. The cells, too, are crowded closely together. In contrast to this is the lightly stained spermatocyte region, due to the fact that here the cells contain a greater amount of cytoplasm in proportion to the amount of nuclear material. The cells have increased so greatly in size in the later generations that the cysts are larger. Usually a characteristic barrier exists between the two main regions of divisions. This is formed by cysts of cells undergoing the process which has been designated as synizesis, a detailed description of which will come later. In almost every instance, too, the line of separation is emphasized by the presence of many cysts of degenerating cells with their spherical masses of chromatin.

OBSERVATIONS ON THE SPERMATOGONIA.

From a study of polar views of the equatorial plate the number of spermatogonial chromosomes was determined to be twenty-one, and in no case was there observed a departure from this characteristic number. The chromosomes in young cells are larger than those in older cells and do not exhibit the tendency to coalesce so readily. Consequently cells for studying the number, form and behavior of the chromosomes were comparatively few, although enough were found to leave no doubt in the observer's mind as to the correctness of these observations and their interpretation. Figures 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, show polar views of the equatorial plate from spermatogonial cells. Certain elements of the complex exhibit constant and striking characteristics in size relationships. The largest three chromosomes in each group are easily identified, as are also the smallest two. The remaining members of the group more nearly approximate each other in size, so no attempt was made to homologize these in the several cells.

The form of the chromosomes varies from spherical and ellipsoidal to kidney-shaped with variations in size and position. The smallest two elements show the most striking differences in these respects from the other members of the group. There seems to be no fixed arrangement of the individual elements, except that there is an evident pairing of twin chromosomes. Sutton reported the presence of similar pairs in *Brachystola magna** and his observations have been verified by other workers in this laboratory on other species of the Orthoptera.† One element of such a pair is considered to be of maternal origin and the other of paternal origin. The tendency for equal elements to get together is very marked even in young cells, and makes conspicuous the presence of an unpaired element, one of the largest three chromosomes. Should its mate exist in the cell it could not possibly be overlooked when even the smallest elements are so prominent. Owing to uniformity in size, precisely which of the three is the unpaired element may be decided upon only when two of them are unmistakably paired. The smallest two elements show this tendency but rarely, their behavior at this stage being consistent with subsequent irregularities.

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* "Spermatogonial divisions of *Brachystola magna*." Kansas University Quarterly, vol. 9, No. 2, 1900.

† The Chromosome complex of *Syrbula admirabilis*, W. R. B. Robertson. Kansas University Science Bulletin, vol. IV, No. 13, 1908.

All of the chromosomes lie with their long axis in the plane of the equatorial plate, and from a study of lateral views of this stage it is evident that the plane of the split in the chromosomes coincides with the same plane. Ideal conditions for equal division of chromatin are therefore present. Division is simultaneous throughout the group. The separated halves move toward opposite poles, maintaining their relative positions until the pole is nearly reached. Thus the shape of the spindle during anaphase is altered to accommodate the varying conditions. See figures 12, 13 and 14. There is no evidence as to the method of spindle-fiber attachment, and it is doubtful whether the matter can be decided in this material. Figure 15 is a drawing of a section through an entire cyst. Most of the cells are in metaphase. A few are in anaphase. The polarity exhibited in this section is typical of all cells of this generation.

In lateral views of anaphases in young cells the chromosomes are distinct. In the older, more crowded cysts the tendency of the individual elements to coalesce produces the appearance of a solid band of chromatin in the equatorial plate. Later stages of the same show two separate bands with spindle fibers between. The plate arrangement is lost when the pole is reached. Figure 17 shows a polar view of an early telophase. The chromosomes have not yet lost their identity, although they have apparently begun to disintegrate. Between the telophase and the succeeding metaphase there is an increase in the amount of chromatin. The formation of a nuclear membrane and the further dissolution of the chromosomes follow. A typical telophase from a young cyst is shown in figure 18. The daughter nuclei are flattened, but assume a spherical outline as the diffusion of chromatin proceeds. Figures 19 and 20 show the culmination of this process.

The inauguration of the next mitotic cycle is marked by the appearance of an exceedingly long and much coiled spireme, whether continuous or not it is impossible to say. At any rate, after the thread has thickened and shortened considerably it is plainly seen to exist in segments which finally condense to form the homogeneous bodies of the chromosomes. Figures 21 to 28, inclusive, show the successive steps in this transformation. The shortening segments show various twists, bends and contortions. See figures 22, 23, 24 and 25. Not until very late in the prophase does the longitudinal split in the threads become visible. (Figs. 26 and 28.) At this stage pairing of equal elements is very common throughout the spermatogonial generations. Note the marked pairs in figures 1, 2 and 4, plate LXV. It would seem from this that throughout the history of the spermatogonial cells there is a consistent provision for the final processes which mark the transition from spermatogonia to spermatocyte. This process is called synapsis. The cells of a mature spermatogonial cyst have not been counted, but judging from the number of cells in a cyst of developing spermatids, eight mitoses complete the activity of the germ cells as spermatogonia, that is, that after the last division there are 256 cells in a cyst. In such cysts the cells are poor in cytoplasm.

After the final division the typical telophase is replaced by synizesis. During this process the chromatin is contracted into a deeply staining granular mass whose position within the nucleus is either central or slightly eccentric, leaving the peripheral area clear. It is quite certain that the chromatin mass is composed of intimately associated granular threads, for occasionally ends protrude from the knot, although entire threads can not be traced. (Figs. 30, 33.) It is true that the chromatin enters synizesis in the form of individual threads, and the presynizetic stage is characterized by the same elements. It is reasonable to suppose that the threads continue as such during the period of synizesis. That some change is taking place within the knot is shown later, but there is no evidence to show that this change involves the disorganization of the chromatin threads and its reorganization into new elements. Nothing can be said in regard to the duration of synizesis. That an end to end conjugation of the paired elements of the spermatogonial nucleus occurs during this period seems established beyond a doubt.

At one side of the conjugating threads lies a definite chromatin body of homogeneous consistency. Occasionally this body shows an uneven outline suggesting a slight disintegration of the constituent chromatin. Its position is constant and it is invariably present. From a study of subsequent maturation processes it is shown to be the accessory chromosome (McClung, Orthoptera) and can be identified as the homologue of the unpaired element appearing in the spermatogonial metaphases. In studying the history of this odd member of the complex, drawings of it in that stage were made, as well as in numerous subsequent stages, for size comparisons. Fig. 14, plate LXVI, shows several drawings from different individuals. The spermatogonial cells from which drawings of the accessory were made vary in age, and as there is undoubtedly a decrease in the chromatin content of these nuclei as the cells multiply we would naturally expect to find homologous chromosomes varying in size in the same individual. The position of the chromosomes with respect to the equatorial plane varies previous to division, that is to say, in the formation of the equatorial plate the chromosomes may lie obliquely to the plane of the equator, and this would cause apparent differences in the size of camera drawings. Conceding that these possible causes of size variation are sufficient to account for the slight variations in size of the accessory as shown in the drawings, we are forced to conclude that the size of this element in the spermatogonia is strikingly constant. A similar study of the homogeneous body observed in the nucleus during synizesis shows a like constancy in size. Although these two elements which appear at different times in the nucleus are so unlike in form we cannot but consider them as equal chromatin masses. Moreover, if synapsis is a conjugation of twin chromosomes, obviously the unpaired element of the earlier stages would take no part in this process. This evidence is sufficient to incline us to believe that the two masses are identical. Further evidence will be given to strengthen this conclusion. An account of the presynizetic stages or growth period will be given in the observations on the first spermatocyte generation.

The First Spermatocyte.

The earliest condition of the spermatocyte cell is the result of the disentanglement of the chromatin knot formed during synizesis. Even before the chromatin has spread to the nuclear membrane, and while the peripheral area is comparatively free from it, it is easy to determine that the chromatin exists in the form of granular threads or rods. See figures 1, 2, 3 and 4, plate LXVI. This diffusion of the chromatin threads makes possible the detection of a second body similar in size and staining qualities to the chromatin body described as present during synizesis. This body is not present before synizesis, is not apparent during the synizetic period, and is present afterward in the interior of the nucleus. The natural conclusion then is that this is a product of synizesis. Its staining qualities indicate that it is composed of chromatin. The distinction between this and the accessory is only possible when the accessory lies close to the nuclear membrane, which is its usual position. In this respect it resembles the accessory chromosome of the first spermatocyte prophase of the Orthoptera.

The history of the three distinct nuclear components, active chromatin, accessory chromosome and plasmasome, will be followed separately up to the spermatocyte metaphase, beginning with the chromatin. The reorganization of the nuclear chromatin into typical spermatocyte chromosomes after diffusion is completed gives no hint of a reversal of the mitotic cycle. That is, the appearances which characterize chromosome reconstruction do not suggest a reversal of the changes which were observed to take place in the diffusing chromatin. The straight threads which typify the early prophase (figs. 1-4, plate LXVI) gradually elongate and finally are disposed into a fine reticulum at the intersections of which are very slight accumulations of chromatin. See figure 4, plate LXVI, and figure 4, plate LXVII. This might be considered as the climax of diffusion, for in this stage the chromatin is most evenly distributed throughout the nucleus. Subsequently there are more extensive accumulations of chromatin at certain points within the nucleus. These amorphous aggregations of granular chromatin gradually assume the form of loosely organized tetrads resembling a few of the types of tetrads found in the Orthoptera. Figure 16, plate LXVI, shows four types of tetrads taken from one cyst all of the cells of which are in the same stage of development; (*a*) shows the largest form. By analysis it is seen to be composed of four equal chromatids and represents the pair of the largest spermatogonial chromosomes conjugated. The disposition of maternal and paternal chromatids is indeterminable in this as well as in the forms shown by (*b*) and (*c*), which are different types of the cross. In each case two opposite arms of the cross are composed of portions of maternal and paternal threads lying parallel to each other. The ends of these arms are the synaptic ends of the chromatids, but whether the synaptic end of a chromatid represents the polar end, as is certainly the case in the Orthoptera,* it is impossible to determine. One of the other pair of opposite arms is composed of parallel maternal threads and the remaining arm consists of parallel paternal threads;

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* Pinney, Edith, Organization of the Chromosomes in Phrynotettix magnus, Kansas University Science Bulletin, vol. IV, No. 14, 1908.

(*a*) shows a rod form in which the division at right angles to the long axis may or may not separate elements of opposite parental origin. It is impossible to ascertain whether these rod forms have passed through the cross stage, since some of the earliest recognizable tetrads have this form and keep it as they condense.

The manner in which these forms are evolved from two conjugated chromosomes of opposite sex, each split longitudinally, is similar to that described for the Orthoptera by McClung;* (*d*) is an unusual condition at this stage of the smallest spermatogonial chromosomes. Even in stages as late as those shown in figures 22 and 24, plate LXVI, the separate halves of this pair often lie on opposite sides of the nucleus. Just previous to the metaphase they approach end to end. The constriction between the two halves is never obliterated by a close union. Evidently synapsis has had no effect on the smallest two members of the spermatogonial complex, although they undoubtedly entered into the synaptic knot. Subsequent changes consist in the condensation of these filiform tetrads to form the homogeneous elements of the metaphase. As the chromosomes approximate the homogeneous condition they arrange themselves at the periphery of the nucleus. This tendency may account for the characteristic position of the accessory during synizesis, the growth period and the spermatocyte prophases. The same nuclear membrane which is formed previous to synizesis continues to function up to the time of a late spermatocyte prophase. At the latter stage there are present within the nucleus thirteen distinct bodies. Figures 10 and 11, plate LXVI, show two parts of the same nucleus appearing in adjacent sections. The thirteen bodies are drawn. These must represent the twenty-one spermatogonial chromosomes plus the plasmasome created during synizesis.

Before stating the homologies between these spermatocyte structures and those of the previous generation the history of the accessory will be followed, beginning with synapsis. In this connection the behavior of the new spermatocyte element, the plasmasome, will be reported. The time of appearance, the nature and source of these two bodies, have already been spoken of. It has also been mentioned that immediately after synizesis the two bodies are practically equal in size. In the succeeding diffusion stages the plasmasome increases in size and the distinction between it and the accessory becomes very marked. In these stages the accessory remains closely appressed to the nuclear wall while the plasmasome is located internally. See figures 3, 5 and 6, plate LXVI. This period during the diffusion of chromatin and the growth of the plasmasome can not be considered as belonging to the prophase of the first spermatocyte. The nucleus increases steadily in size, reaching its maximum when diffusion is complete, so we may consistently call this interval after synizesis the growth period. Its culmination marks the installation of important changes, one of which, the re-formation of the chromosomes, has already been described. The accessory meanwhile maintains its former position, size and staining qualities. During the prophase the plasmasome gradually diminishes in size, and finally disappears just before the metaphase. During this time, too, it does not stain so readily with chromatin stains. In the Heidenhain's iron-hæmatoxylin preparations the staining quality of the plasmasome varied with the amount of extraction in the iron-alum solution. Occasionally the plasmasome presents a vacuolated appearance. This may occur at any time during its history but is more characteristic of the beginning of its dissolution. Occasionally in the prophase there occur two small homogeneous bodies staining like the plasmasome. As the typical plasmasome is absent and the accessory present these are considered as fragments of the plasmasome. There is no regularity in their occurrence. The cysts in this condition are not frequent and the majority of their cells contain typical plasmasomes.

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* McClung, C. E., '00, The Spermatocyte Divisions of the Acrididæ, Kansas University Science Bulletin, IX, 1, '02; The Spermatocyte Divisions of the Locustidæ, ibid., XI, 8.

In later stages the plasmasome is identified by its shape, becoming spherical as it decreases in size. Figure 7, plate LXVI, shows a nucleus containing the plasmasome and the accessory. The difference in staining qualities is apparent. The accessory remains in its former position, its form to the observer depending on his point of view. Plate LXVII consists of a series of drawings showing the size relations of the accessory and the plasmasome at the time of synizesis, the growth period and the succeeding prophases. The drawing of nuclei at the top of the page show the condition of the active chromatin. They are numbered in the order of the changes which they present. For instance, figure 1 shows a nucleus during synizesis. The perpendicular column below figure 1, designated 1*a*, shows a number of drawings of the accessory taken from cells in the same stage as figure 1. Figure 2 shows a nucleus of the stage immediately following synizesis. The perpendicular column, 2*a*, below figure 2 shows a number of drawings of the accessory taken from nuclei in the same stage as figure 2. The perpendicular column, 2*b*, beneath figure 2 shows a number of drawings of the plasmasome taken from cells in the same stage as that shown in figure 2. In the same way columns 3*a* and 3*b*, 4*a* and 4*b*, etc., are drawings of the accessory and plasmasome from nuclei such as are shown in figures 3, 4, etc., respectively. The horizontal columns *A*, *B*, *C* and *D* indicate the different individuals from which the drawings were made. The differences in size which are shown in these monoplane drawings depend upon the point of view of the observer. That the accessory is constant in size is easily determined by different focusings. From these drawings there is also found to be a regularity in the relation between the size of the plasmasome and the condition of the active chromatin of the nucleus. From the foregoing observations it is now clear that the thirteen nuclear structures present in the late spermatocyte prophase comprise one accessory, one diminished plasmasome, two small chromosomal elements of opposite parental origin, and nine ordinary tetrads.

Figures 1 to 10, inclusive, plate LXVIII, show typical polar views of the first spermatocyte metaphase. All of the groups shown are from different individuals, with the exception of figures 2, 3, 4, plate LXVIII, which were in the same section of the same cyst. As many as six of these views, all typical, have been observed in one section in one cyst. There are eleven chromosomes present, each of which, with the exception of the accessory, is composed of four chromatids. The plasmasome has disappeared, also the nuclear membrane. The chromosomes lie in a clear area surrounded by the cytoplasm. Nine of the complex, including the largest, form a rather compact ring, in the center of which appears the smallest member of the group. The relative positions of the chromosomes forming the ring vary. One chromosome lies outside of the ring. Figure 11, plate LXVIII, shows six of these outer chromosomes at this stage taken from the same individual from which figure 6 was made. So, also, figures 12, 13, 14 and 15 are drawings of the similarly located chromosome found in the individuals from which figures 7, 8, 9 and 10, respectively, were made. This eccentric member shows remarkable constancy in size. Its size and its position suggest the accessory during synapsis. See figures 29, 30, 33, plate LXV. Figure 5, plate LXVIII, shows a polar view of an atypical metaphase. This condition was observed only twice in this material, both times occurring in different individuals. There appear to be twelve chromosomes present. In addition to the small chromosome within the ring, there are two large equal elements which are not large enough to correspond to any elements present in the typical metaphase. Only eight chromosomes form the ring. It must be that the missing one of the nine which usually form the ring is represented by the two small and unusual bodies which lie within the ring, one on either side of the small element, and that this is merely an accidental case in which synapsis did not occur. In connection with this supposition we recall the fact that synapsis did not occur in the small chromosome at the usual time. This similarity of action during the synaptic period may be significantly related to their similarity of position.

In a lateral view of a spermatocyte anaphase the same surface of the chromosomal elements is presented to the observer as is seen in the equatorial plate of the spermatogonial cells. By referring to figures 1 to 10, plate LXV, it will be seen that the chromatids have become slightly shorter and correspondingly thicker. Here again the smallest chromosome asserts its independence. In the spermatogonial cells these small chromosomes present spherical outlines. In the first spermatocyte generation, instead of shortening, as their fellows, they have elongated. Only in this element and in the accessory was the plane of division actually determined. Since the two halves of the smallest chromosome are never so closely united that we lose sight of their identity, it can be stated positively that division in this case is transverse and qualitative, causing the separation of maternal and paternal elements. Owing probably to the slight attraction exhibited between the halves of this chromosome division is effected while the other chromosomes are still intact. Lateral views of early anaphases invariably show this condition. Similar views of later stages show its separated halves preceding the larger diads to the poles. In the ordinary tetrads the formation of the crosses might be interpreted to have the same significance as is attributed to the like form in the Orthoptera, in which McClung has shown conclusively that the first division plane is longitudinal. However, in this case there is no positive evidence to offer. The chromosomes enter the equatorial plate with their longitudinal axes parallel to the spindle fibers. Figures 16 and 17, plate LXVIII, show that the polar ends of the chromosomes converge toward the poles of the spindle. That both methods of division may be employed by different members of the group is shown by a study of the accessory at this stage. This element, which is composed of two chromatids, was last observed in the metaphase lying outside of the ring. The element (x) in figure 16, plate LXVIII, is undoubtedly the accessory chromosome. This drawing is not limited to one plane. The small chromosome is shown dividing in its usual manner. This element, it will be remembered, is located at the center of the ring and no element of the ring could lie so far from this center as the one marked (x). This, then, must lie on the outside of the circle. From the arrangement found in polar views of the metaphase one would expect in the lateral views to find sections which would show four chromosomes in the same plane. These would include the small central member, two chromosomes of the ring, one on either side, and, at one side, the accessory. Such a section is shown in figure 17, plate LXVIII. The small chromosome, it will be seen, occupies the axis of the spindle, which in this view appears asymmetrical, the asymmetry being due to the extra divergence of the fibers attached to the accessory.

In these lateral views of anaphases the structure of the accessory is easily determined. It is composed of two chromatids, which are shown in figures 19, 20 and 21, plate LXVIII. All of the other chromosomes contain four chromatids, although in some only two of the four appear in the same plane. The accessory is easily identified by its form in these stages, where it is shown to divide tardily, division not beginning until the ordinary chromosomes have entirely divided. In their journey to the poles the accessory chromatids lag behind the others. Figures 17 to 26, plate LXVIII, show this behavior at different stages. All of the chromosomes of the complex keep their relative positions until the pole is reached. Figures 1, 2, 3 and 9, plate LXIX, show polar views of the dividing groups with the inner and outer members in their characteristic positions. As soon as the pole is reached the chromosomes crowd together and, on account of the lagging of the accessory, lateral views of this stage show the condition reproduced in figures 25 and 26, plate LXVIII; (x) is the accessory. It is easily identified in both daughter groups. Figure 24 shows the only case observed which might be interpreted as the failure of the accessory to divide. The spherical form of the structure (x) may indicate a degenerate form of the accessory or an unusually persistent plasmasome. The crowding together of the diads at the poles completes the cycle of changes occurring during the first spermatocyte generation. No telophase involving the disintegration of the chromosomes and the appearance of a new nuclear membrane occurs.

The Second Spermatocyte.

The second spermatocyte generation begins with the formation of an equatorial plate by the members of the new spermatocyte nucleus. These second spermatocyte chromosomes consist of ten diads and one monad or single chromatid, the accessory. In figures 1, 2, plate LXIX, of typical equatorial plates of this generation will be seen a tendency toward the same chromosome arrangement which prevailed during the preceding mitotic cycle. From the size relations shown in figure 4, plate LXIX, which is a group of accessory chromosomes from cells of the same stage and animal as figure 3, plate LXIX, respectively, we are justified in our conclusions as to the identity of this element. Figures 5, 6 and 7, plate LXIX, are polar views of beginning anaphases. The chromosomes are viewed here in cross-section. Figures 10, 11 and 12, plate LXIX, show lateral views of the beginning of this ultimate division. Figure 10 suggests what transpired between the stage shown in figures 1, 2 and 3 and that shown in figures 5, 6 and 7. The transition is extremely brief, for evidence of it is comparatively infrequent. The chromatids which, during the first spermatocyte division, lay parallel to each other have separated at one extremity and have swung around until they lie end to end, the separate ends pointing toward opposite poles. The chromatids maintain this position during a relatively long period of time, for this condition and the following telophase are most commonly noted in cysts of second spermatocytes. A typical spindle is formed and the fibers are attached at the separated ends of the chromatids. Separation of chromatids occurs simultaneously, the smallest member here acting in unison with the others. This may be regarded as due to the fact that the same conditions are present in all of the chromosomes previous to division; that is, the degree of union between the chromatids is the same in each diad, while it will be remembered that this relation between the diads which composed the tetrads of the first spermatocyte varied.

When the chromosomes separate sufficiently to expose a clear zone of fibers in the region occupied by the equatorial plate we find the accessory chromatid still in its place, and it keeps this position until the remaining chromatids have almost reached the opposite poles. Figures 13 to 18, inclusive, plate LXIX, show the successive steps in this division. Well coalesced daughter groups of this division are observed at opposite ends of the spindle, while the accessory lingers half way between. The accessory finally approaches one of the groups and almost immediately the dividing cell wall is formed. This leaves the accessory near the newly formed cell wall, entirely apart from the group to which it evidently belongs. Figure 19, plate LXIX, is a group of such bodies drawn from cells in this stage. The size of this lagging body was thus found to be constant. The spindle fibers between the two groups persist until after the nuclear membranes of the daughter cells are formed. Before this occurs, however, the changes shown in figures 20 to 25, inclusive, plate LXIX, take place. This consists in the withdrawal of the accessory from its position near the dividing wall into the now shapeless chromatin mass of the new nucleus. In studying these processes it was very easy to obtain sections which showed the two daughter cells in the same plane. The connecting band of spindle fibers leaves no doubt as to their relation even after the new cell wall has been formed. The accessory occurs in only one of these cells. A further significant fact is that in every such case where both daughter cells can be identified beyond doubt one always shows the accessory at some stage of its characteristic activity, while in the other no corresponding body is to be found.

As soon as the membrane forms around the spermatid nucleus which contains the accessory this element becomes detached from the mass of which it forms a part and moves again to the nuclear wall. Its individuality again becomes prominent. Figures 26 to 31, plate LXIX, show this condition. Here also the same precautions in determining its identity were observed.

Care was taken to study both daughter groups, in one of which it invariably occurred while the other offered no evidence of the presence of a similar element. The constancy in size of the accessory and the relation of its size here to the size of the accessory as determined by figures 4 and 19, plate LXIX, help to establish its identity. This condition of the chromatin in the spermatid nucleus lasts for only a short time. The large chromatin mass soon begins to break up into smaller masses which eventually distribute themselves against the nuclear wall. In an early stage of this disintegration the accessory is still easily recognized, as it lies on one side of the nucleus apart from the rest of the chromatin. It still keeps the elongated form it displayed in the second spermatocyte anaphase.

A whole cyst of young spermatid nuclei was counted in order to determine in just what proportion of the spermatids of one cyst the accessory occurred. The importance of this observation is obvious, although it seems that the result could be predicted safely from the evidence obtained from previous observations. An account of the method used in counting may help to verify the results. Serial sections of an entire cyst were obtained. The cyst chosen for counting ran through twenty-four sections. The sections were five micra in thickness. The exact condition of the chromatin was found to vary in almost every cyst of this generation. In the cyst counted were found the stages shown in figures 28, 29 and 31, plate LXIX. From the conditions existing in such nuclei we would expect to be able to identify the accessory from its shape and its position with respect to the rest of the chromatin in the nucleus. Evidently the number of nuclei in such a cyst and the number of spermatids formed would be equal. All whole nuclei or almost whole nuclei and fragments containing the accessory were counted. It was impossible to avoid the error of counting one nucleus as two where a nucleus happened to be cut exactly in half; one half appearing in two adjacent sections. The number of nuclei containing the accessory was 484. The number of fragments of nuclei which contained the accessory was 40. Thus the entire number of spermatids in which the accessory occurred was 524. The number of nuclei counted which contained no accessory was 577. These, however, would include the nuclei from which small fragments containing the accessory had been severed.

That would make the number of nuclei with no accessory 537, which is slightly larger than the number with the accessory. It has been pointed out that the nuclei which were cut in two equal parts might be counted as two. This would add to the number of cells which did not contain an accessory. Considering this source of error the number of cells of each kind may practically be considered as equal. There can be no doubt as to the occurrence of two kinds of spermatids which develop into spermatozoa, one containing one more chromatid, the accessory, than the other; and from the evidence presented we feel justified in concluding that the two kinds of spermatozoa occur in equal numbers.

III. A COMPARISON OF THE RESULTS OF STUDIES UPON CHROMOSOMES OF ANASA.

BY C. E. M'CLUNG.

1. *Methods.*

The methods of an investigator are a very important factor in arriving at conclusions, and it is quite possible to secure diametrically opposite results upon the same material by varying the technical processes. It will, therefore, be necessary to consider the methods of preparation and study employed upon *Anasa*. Paulmier, Montgomery, Wilson, Lefevre, McGill and Pinney fixed their material with Flemming's fluid, corrosive-acetic mixtures, Bouin's fluid and various other cytological reagents. This material was then sectioned in paraffin, and stained, principally with the iron alum—hæmatoxylin stain of Heidenhain. The slides thus prepared by Paulmier, Wilson, Lefevre and Pinney are beautiful examples of cytological technic and leave little to be desired in delicacy and precision. A considerable number of the slides sent me by Professor Wilson and Professor Lefevre are prepared according to the methods of Foot and Strobell, so that I have been able to study the material under their conditions, although, unfortunately, their own preparations have not been accessible to me. Since the entire case of these investigators, as opposed to all their fellow workers, rests upon their own peculiar methods, it seems desirable to consider in detail the technic upon which they rely.

The usual methods of cytologists are dismissed with practically no consideration, and instead of fixing the material, it is spread upon glass slips and allowed to dry. (Foot and Strobell, '07, p. 282.) In this condition it is stained with Bismark brown and mounted in balsam. Entire reliance is placed in this method, and little attempt is made to correlate the results thus obtained with the appearances presented by other systems of technic. That the position of these authors on this point may be clearly understood, I quote their statement of the case.

"Professor Wilson, in his recent paper in *Science,* February, '07, replying to our preliminary note, says that he thinks the contradiction in our results is probably due to the difference of method employed, we having placed our faith in smear preparations, while he has relied on sections. We are glad of an opportunity to emphasize this faith, believing that for demonstration of the structure and count of chromosomes our modified smear preparations are more reliable than sections; and it is for this reason we have abandoned the use of sections in studying chromosomes, except for comparative work and for studying the topographical relation of the cells. In cells fixed and sectioned nearly all the delicate details shown in the chromosomes of our smear preparations are completely lost, and it ought to be too obvious to mention that a method which presents clearly each individual chromosome in its integrity offers decided advantages when the question of accurate counting assumes the importance and develops the contradictions familiar in recent literature."

The authors state that they have used sections for comparison and topographic work, but none of their photographs are made from sections, and their entire argument, as published, is based upon material prepared according to their own method.

It is my judgment that this method, *used alone*, is entirely inadequate for accurate results, and in this particular case is responsible for the discrepancy between these investigators and Paulmier, Wilson and Montgomery. From the work of Miss Pinney it will be clear, I think, that in the prophases figured by Foot and Strobell there are two darkly staining bodies, the accessory chromosome and the plasmasome, instead of the one shown in their photomicrographs. Owing to the technic employed by them the plasmasome is practically destroyed, and instead of using other methods to determine the nature of the nuclear body, they *assume* that it is a plasmasome. "As the presence of a plasmasome in the nucleus at these stages is the typical phenomenon familiar in all known forms (its absence being most exceptional), we feel justified in interpreting the structure we find in the resting nucleus as a true plasmasome, and not an odd persisting spermatogonial chromosome, *i. e.*, chromosome nucleolus." (Foot and Strobell, '07, p. 284.) Further, the smear method does not give precise and accurate pictures of the chromosomes. The variation in size, owing to the different thicknesses of the smear and amount of spreading, is very extensive, as may be seen by a comparison of the photomicrographs of Foot and Strobell. Compare, also, figures 21-26, plate LXX, which represent smears of cells in the same stage. Not only may the entire groups of chromosomes in similar cells vary as three or four to one, but the members of one cell may suffer unlike expansion or contraction to a similar extent, if the conditions of drying are variable, due to the thickness of the smear film. There is but one advantage of the smear method over sections, and that is that it presents all the elements of the cell in one plane, so that their entire outline is visible for studying and photographing. It is a method that should be used in connection with sections, and from the beginning of my work I have utilized it consistently and with great profit in this way. I therefore speak of it as a warm friend and advocate, but at the same time I realize its limitations and am convinced that it should not be used to the exclusion of all other methods.

Foot and Strobell have employed photography alone as a means of presenting illustrations of their material, and it is assumed by them that if a thing can be photographed it must necessarily be a true picture of normal conditions. This I consider to be a decided fallacy. A photograph is an interpretation by the observer, just as is a drawing. The personal factor is no more absent from one method of illustration than it is from the other. Photographs may present with greater fidelity the details of structure in an object, but the choice of the object and the nature of details are at the command of the photographer. It is possible, especially in smear preparations, to select cells that will illustrate almost any condition and to photograph them. The highly interpretative character of the photograph is illustrated admirably by the present controversy over the chromosomes of *Anasa.* Foot and Strobell publish photographs that seem to show that the accessory chromosome divides in the second spermatocyte division. This is their interpretation of the behavior of this element, and they illustrate it by photography. Not a picture which they publish would indicate that there is ever a case where the accessory chromosome positively fails to divide at this time, and yet literally thousands of unquestionable cases of this occur in every good preparation. See the group of cells shown in figure 15, plate LXXI. By selecting a series of early anaphases, and a very few obscure and distorted individual cells, they are able to secure pictures which appear to bear out their contention. In speaking thus of the methods of Misses Foot and Strobell, I wish it clearly to be understood that I am not reflecting upon their motives. It is my desire only to show that photographs are interpretations of observed phenomena and have no claim to infallibility. Again, as in the case of the smear method, I would state that I speak as a friend of the method and not as one who deprecates it. I believe that scientific papers, particularly cytological, should, whenever possible, be illustrated by photographs, and in my own publications I have followed this plan so far as the circumstances would permit.

2. *What is the number of spermatogonial chromosomes and of oögonial chromosomes?*

Confessedly, the accurate estimation of the numbers of chromosomes in these generations of cells is a difficult matter, and if it were the only means of determining the chromosomal differences of the sexes there might be occasion for doubt with regard to theories founded upon such enumerations alone. Fortunately, it is only one of several criteria of sexual differentiation in the germ cells, and so is not of commanding importance. Accurate counts of the chromosomes, however, are entirely possible with care, and concordant results are obtainable by independent observers. In the case of *Anasa* this is quite possible, and both Miss Pinney and myself have found the number twenty-one uniformly present in the spermatogonia. Not a single instance of twenty-two chromosomes was found in any spermatogonium, and we must therefore conclude with Wilson that thirty-one is the normal spermatogonial number. In plate LXX, figures 1-3, may be seen spermatogonial complexes showing this number clearly.

It is claimed by Foot and Strobell that the number is twenty-two, and they publish four photographs in support of this view. Only one of these represents a stage where the chromosomes are compact and homogeneous, and this shows twenty-one chromosomes, although in the explanation of the figure the authors state that one of the apparent chromosomes is really two joined at right angles. Since there is no case in the figure where one chromosome is bent at almost right angles, the explanation is not very convincing. The remaining three are of earlier stages, in which the chromosomes have a loose structure that might readily be disturbed in the process of smearing, thus separating one of the larger chromosomes. In two of the photographs such an interpretation would seem to be entirely justified. Photo 49 is the only one in which there would seem to be any certainty with regard to the number twenty-two. Here it appears as if conditions were normal, and it might be recorded as an instance of twenty-two chromosomes in the spermatogonia.

The conditions regarding the spermatogonial number may be summarized thus: Paulmier, Montgomery at the time agreeing with him, reported twenty-two spermatogonial chromosomes. Later, Wilson, working upon Paulmier's original preparations in part, finds twenty-one spermatogonial chromosomes, and Montgomery, restudying his own material, agrees with this enumeration. Lefevre and McGill report twenty-one spermatogonial chromosomes from their own preparations. Foot and Strobell, working upon smear preparations, consider twenty-two to be the normal spermatogonial number. Miss Pinney, upon examining material from Kansas, Massachusetts and Pennsylvania, and working without a knowledge of others' results, finds twenty-one to be the spermatogonial number. Finally, from a study of the original material of Paulmier, Wilson, Lefevre and McGill, and Pinney, I myself find in all clear cases, where there is no doubt of the presence of all the chromosomes, that the number is twenty-one. Foot and Strobell object to the testimony of Montgomery, and of Lefevre and McGill, on the ground that they reported at one time an even number of spermatogonial chromosomes and at another an odd number. It must of course be admitted that this weakens their testimony, for it is an evidence either of careless work or of the influence of preconceptions. I can recall with what difficulty I persuaded myself, against the current conceptions of chromosome numbers, that the spermatogonial number of chromosomes is odd in the Orthoptera, and I can easily understand the temptation, in an early stage of an investigation, to seek concordance with accepted opinions. The investigators who reported even numbers for their material did so when all the evidence from other forms seemed to demonstrate the universality of this phenomenon. In a sense their testimony is more valuable after a restudy of their material, because it indicates the desire to arrive at facts regardless of consequences. It is a very unusual man, or a very stubborn one, who finds no occasion to change his opinions.

This is the present status of the question concerning the spermatogonial number of chromosomes in *Anasa.* If it is impossible for the interested cytologist to come to a conclusion regarding the facts of the case from the studies so far made, he is quite at liberty to undertake an investigation for himself and I have no doubt but that all the material that has been available for my investigation will be placed at his disposal.

There appears to be no dispute regarding the oögonial number, although the counts in these cells have been less numerous than in those of the male. So far as the opportunity has offered I have gone over the female complex of chromosomes, and I have no reason to doubt that the number is twenty-two, as determined by Wilson.

3. *What is the number of first spermatocyte chromosomes?*

Regarding the number of first spermatocyte chromosomes, there seems to be no difference of opinion, since every observer has recorded eleven as typical for this generation. The clearness with which the chromosomes of the first maturation mitosis appear in the equatorial plate almost precludes the possibility of error. Here also may be found a close adherence to a type of arrangement which presents the small chromosome in the center, surrounded by a more or less regular ring of nine chromosomes upon the outside of which is placed the accessory chromosome. This is not an invariable arrangement, for it is a culmination of the movements of the chromosomes in the prophase where the elements bear somewhat similar relations to each other, but it appears in a large proportion of the cells.

The position of the accessory chromosome upon the outside of the group has led Foot and Strobell to coin another new name for it, and in their terminology it is the "eccentric chromosome."

4. *What is the behavior of the accessory chromosome and of the plasmasome in the first spermatocyte prophase?*

While there is no dispute regarding the number of chromosomes in the first spermatocyte, there is serious divergence of opinion with reference to the structure of the accessory chromosome. Upon its nature depends the number of spermatogonial chromosomes and the character of the four spermatids derived from each first spermatocyte, so its determination is most important. If it be a tetrad then the spermatogonial number must be even and the spermatids all alike in the possession of eleven chromatids; but if, on the contrary, it be a diad the spermatogonial number of chromosomes is necessarily odd and the spermatids of two types, one of which possesses eleven chromosomes and the other ten.

With the exception of Foot and Strobell all observers are agreed that there are but two chromatids in the accessory chromosome, but these observers claim that it possesses four as do the other chromosomes. As proof for this contention, they publish a series of chromosome groups from the late prophase in which the various elements are clearly shown. The identification of the accessory chromosome is correctly made in each case, I believe, but it is entirely clear to my mind that there is nothing in the appearance of these photographs to justify the interpretation of the accessory chromosome as a tetrad. There is in each case a characteristic difference between the tetrads and the accessory chromosome, for in the former there always appears a diamond-shaped opening, the angles of which point to the two lines of cleavage, while in the case of the accessory chromosome this is lacking. Every accessory chromosome, on the contrary, shows a clear, straight line of division along its entire length. In but a single instance is there an exception, and that is in their figure 4, plate II, where the plane of longitudinal cleavage is interrupted by transverse markings. A careful examination of this chromosome will demonstrate, however, that there is not only *one* of these apparent cross divisions, but *two* of them. I am convinced that the excellent photomicrographs of Foot and Strobell of this stage are sufficiently clear in their evidence of the nature of the accessory chromosome, and I have not included any number of these stages in the photomicrographs accompanying this paper. Moreover, in none of the material that I have examined is there any indication whatever of a tetrad structure in the accessory chromosome, and I am thoroughly convinced that it is a univalent chromosome.

If the earlier prophase of the first spermatocyte be examined, the chief error of Foot and Strobell becomes evident. It is claimed by these investigators that the accessory chromosome behaves during the prophase as do the other chromosomes and that there is but a single nucleolus-like body present —a plasmasome. The work of Miss Pinney showing the transition in form and size of the accessory chromosome and of the plasmasome, both of which appear simultaneously in the nucleus, makes it entirely clear that Foot and Strobell were mistaken on this point. As I have elsewhere pointed out, the technic of these investigators is responsible for their failure to find the plasmasome, for it is this structure, and not the accessry chromosome, that is missing from the smear preparations.

These investigators have pointed out the large difference between the appearance of the accessory chromosome in drawings made by Wilson and the photographs illustrating their own paper. Such variations in the form of this element will receive explanation in part from the series of drawings made by Miss Pinney to illustrate the transition in form of the prophase elements. Both the stage of development and the method of preparation influence the form of this accessory chromosome. As a rule, sections show this element as a spheroidal, apparently homogeneous body during most of the prophase, but occasionally, just succeeding synizesis, it appears as a short, thick thread, with a tendency to be bent at the middle. This is the nearest approach to a spireme condition that it attains, and in this corresponds to similar conditions which I have described for certain Locustids. So far as my experience goes it would seem to be the rule that the accessory chromosome, to a certain degree, undergoes a granular diffusion of the chromatin similar to that of the other chromosomes, but that it is less extensive and is frequently marked by the close approximation of divisions of the thread.

It will be observed from plate LXX, figures 4-6 and 11, that the accessory chromosome in this spireme condition is accompanied by a large distinct plasmasome which lies toward the center of the nucleus. Such a structure is absent from the photographs presented by Foot and Strobell when the accessory chromosome (their plasmasome) is elongated. As will be noted in Miss Pinney's description, the plasmasome does not appear until after synizesis is established. Some of the nuclei figured by Foot and Strobell would seem to be presynizetic in development and could not therefore contain plasmasomes.

I would conclude, therefore, that after synizesis there are present in the first spermatocyte nuclei two nucleolus-like bodies, one the accessory chromosome and the other a plasmasome. Further, that the accessory chromosome exists throughout the whole period, for a time, as a short, heavy thread, at other times concentrated into a mass, and finally in the late prophases as a straight longitudinally split rod. The plasmasome, on the other hand, is an inconstant structure, absent before synizesis, and again in the late prophase, and is not to be mistaken for the accessory chromosome.

5. *What is the behavior of the accessory chromosome in the first spermatocyte mitosis?*

Reference has already been made to the condition of the accessory chromosome in the late prophase and to its position in the equatorial plate. It appears in the metaphase as a univalent, longitudinally split rod lying outside the ring of ordinary chromosomes. In division its halves separate and during the anaphase move to the two poles of the spindle as do those of the other chromosomes. Examples of this may be seen in figures 2, 3, 4, 5, 6, 7, 8, 9, 10, plate LXXI. Both series of daughter chromosomes may be seen in plate LXXI, figure 3, which shows a mid-anaphase with the halves of the accessory chomosome accompanying each group. There appears to be no question on the part of anyone regarding the movements of the chromosomes in the first spermatocyte, so that an extended discussion on this point is not called for.

From the fact, however, that Foot and Strobell have used the tardy division of the accessory chromosome in the first spermatocyte as an argument to prove its division in the second spermatocyte, because here also it lingers for some time near the equatorial plate after the other chromosomes have moved toward the poles of the spindle, it will be necessary to call attention to figures 6, 7, 8, 9, 10, plate LXXI. These show that while the time of division is later than that of the other chromosomes the actual separation occurs and the halves of the divided accessory chromosome may, in each case, be seen in the daughter cells. No instance could be observed where there could be doubt of this fact. The clearness of these phenomena is due to the fact that the accessory chromosome remains, as in the prophase, distinct from the other chromosomes, so that it can be followed even into the telophase. As will be seen later, the same aloofness on the part of the accessory chromosome is encountered in the second spermatocyte and is so marked that there is no difficulty in tracing its behavior.

6. *What is the behavior of the chromosomes in interkinesis?*

The interval between the two spermatocyte divisions is comparatively brief and the changes in the relative positions of the chromosomes slight. While the chromosomes mass together, the outlines of the individual elements may be seen clearly in favorable preparations of the telophase. Since the whole daughter chromosome complex travels to the pole at about the same rate, its members at the end of the movement lie at approximately the same level. When therefore the second spermatocyte spindle is formed there is little or no change in the positions of the chromosomes, and the equatorial plate of the metaphase corresponds in general with that of the first spermatocyte, from which it was derived. While this is true, the slight movements of all the chromosomes during their poleward migration usually results in a destruction of the typical ring arrangement so characteristic of the first spermatocyte. Because of its isolated position and somewhat greater variation of movement in the anaphases, the accessory shows more marked differences in position in the equatorial plate than the other chromosomes. If it has moved toward the pole at the same rate as the rest of the complex and maintains its position during the telophase it will then be found upon the periphery of the equatorial plate in the second spermatocyte. If, on the contrary, as often happens, the movement is slightly slower than that of the other chromosomes and it swings around under the mass during the anaphase movements it will later appear within the group of chromosomes in the resulting equatorial plate. It is not possible, therefore, to recognize the accessory in the second spermatocyte by its position, as might frequently be done in the first spermatocyte. I am of the opinion accordingly that any identification based upon position alone is not warranted in the case of the accessory chromosome in the second spermatocyte. By this I do not mean that there may not be similar arrangements of the chromosomes in both spermatocyte metaphases, but rather that the opportunities for movements of the chromosomes during the first spermatocyte anaphase and telophase are so great that no rule may be laid down to mark a type of second spermatocyte. (Plate LXXI, figures 11, 12.)

7. *What is the behavior of the accessory chromosome in the second spermatocyte mitosis?*

At this point in the history of the accessory chromosome of *Anasa* there occurs the wide diversity of opinion between Foot and Strobell and the other investigators who have studied it. The issue is clearly drawn. Foot and Strobell claim that the accessory chromosome is divided in the second spermatocyte as in the first spermatocyte, but Wilson and others are just as positive that it passes undivided into but one of the pair of spermatids formed by the division of each second spermatocyte. Issues are joined here on a question of fact, and it becomes necessary to determine, therefore, whether the accessory chromosome divides in the second spermatocyte metaphase or whether it passes undivided into one of the two daughter cells.

I must confess that it is a matter of no little astonishment to me that there should be any difference of opinion on this point, because the conditions are so clear and unmistakable as almost to preclude error. A number of photomicrographs of the second spermatocyte anaphase have been prepared from both sections and smears and are reproduced in plate LXXI, figures 13-27. In figure 15 there are shown ten pairs of spermatids as they appeared spread upon the glass slip. This slide was prepared according to the method of Foot and Strobell and shows the cells practically separated so that there can be no question of a later division of the accessory chromosome. In each one of these ten pairs it is clearly seen that one member contains an accessory chromosome while its mate lacks it. The same statement holds true of all similar cells drawn and photographed, and of the thousands of others examined. *In no case* *was a divided accessory chromosome found in any second spermatocyte.* For a short time the accessory chromosome lies against the mass of chromosomes, but when the spermatids are separated and the nuclei re-form it moves away again and lies at one side. Such conditions are shown in plate LXXI, figures 20-21, 25-27. No clearer or more precise demonstration of a cytological fact could be asked than is here afforded by the unilateral movement of the accessory chromosome.

The question naturally arises, why, if this be true, should two observers decide that the accessory chromosome *does* here divide? It is of course, impossible to explain just why this has occurred, but it would seem to me that Foot and Strobell were impressed with the necessity of showing every chromosome in both daughter cells and that they chose stages which exhibited such arrangements. Since it is impossible to find these conditions after a mid-anaphase, owing to the massing together of the chromosomes, all their pictures were made in the early anaphase while the accessory chromosome lies in or near the equatorial plate. *Not a single photograph of an unmistakably completely divided second spermatocyte is shown among all their figures.* Since it is only at this time that the accessory chromosome may definitely be demonstrated to occur in only one daughter cell their failure to figure it may be understood.

Since Foot and Strobell base their case upon the evidence afforded by their photographs, it is proper that these should be considered. They show in plate III twenty-three figures of second spermatocyte anaphases and telophases. In all but figure 45 the accessory chromosome lies undivided in the equatorial plate, and in this two independent nuclei with no clearly marked accessory chromosomes are advanced as evidence that the accessory chromosome has divided. Figure 46 shows also two nuclei with no indication that they are daughter derivatives. Figures 29, 30, 31 and 44 are introduced to show the actual division of the accessory chromosome. Figure 29 shows the accessory chromosome of a mid-anaphase with a slight constriction at the center, figure 30 a similar cell with two distorted and ill-defined chromosome masses, figure 31 two other similar daughter groups with an apparently divided lagging chromosome, while figure 44 exhibits a mid-anaphase with the daughter (?) groups widely separated and turned by spreading and a broken accessory chromosome midway between them. In all of these cells the chromosomes are thin and of indefinite outline and have apparently suffered much in the process of preparation. There is not a clear case of a divided accessory chromosome in the series, although individual cells, doubtless the best that could be found, are selected and photographed. That later stages show conclusively the undivided accessory chromosome, not alone in selected cases but in every cell in a microscopical field, is demonstrated in plate LXXI, figure 15, of this paper.

The objection may be raised that such a stage does not show all the chromosomes; but it is not a valid objection because it is impossible to photograph all the chromosomes at this stage on account of their apparent fusion into a mass. Moreover the essential facts are admitted by all. It is agreed that all the chromosomes, with the exception of the accessory chromosome, divide so that each group contains ten ordinary chromosomes; it is agreed that the lagging chromosome is the accessory chromosome. The question therefore to be answered concerns the behavior of the lagging chromosome. Are its derivatives found in each of the separated daughter cells of the second spermatocyte; or is it, undivided, included in only one of the two? The evidence on both sides has been presented in statement, drawing, and photograph and the judgment of those interested must, in the absence of personal study, be based upon the presentations. The crux of the situation lies here, for if the accessory chromosome divides there is no dimorphism of the spermatozoa and no visible sexual differentiation of the paternal germ cells, but if it remains undivided then there is a dimorphism of the spermatozoa and a consequent visible chromosome differential between two numerically equivalent classes.

It is pertinent to consider also whether in evaluating the evidence in this case, any considerable number of genuine instances of unusual conditions can be held to invalidate the common conclusions reached by numerous independent students of these phenomena. There can be no question of the occurrence of abnormal conditions in the development of the germ cells. Entire cysts, or even testes, become degenerate from imperfect coördination in development; certain daughter groups of cells fail to separate and thus produce spermatids with two or four tails and as many simplex groups of chromosomes; minor aberrations occur throughout all stages. Can these be held to prove that there is no constancy in the processes and results of spermatogenesis? Can deviations from the normal or average be regarded as an argument against a type? If so there can be no general laws in biology.

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CONTENTS:

FOUNDATIONS OF ARITHMETIC.................... *Arthur Bowes Frizell.*

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THE FOUNDATIONS OF ARITHMETIC.

DISSERTATION FOR THE DEGREE OF DOCTOR OF PHILOSOPHY, SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL OF THE UNIVERSITY OF KANSAS.

BY ARTHUR BOWES FRIZELL, OF BOSTON.

This thesis seeks a foundation for arithmetic in the ideas underlying Cantor's formulation of his system of ordinal types.

It proceeds by postulating, but follows D. Hilbert and G. Peano rather than E. V. Huntington. The search is for postulates possessing heuristic and didactic, not merely subsumptive value.

A *motif* is found in the notion of an abstract group, which secures the development step by step of all number systems so far studied without further postulates than those needed for the transfinite ordinals.

As axioms are to be avoided, it is necessary to state carefully the definitions and theorems used even when they are well known to the mathematicians, but in this case the proofs are omitted.

1. *Definition.* A set of symbols a, b, . . . will be said to form a K-class if we possess a test which enables us to assert in every case either that $a = b$ or that a is not $= b$ subject only to the restrictions that

a) the result of comparison be uniquely determined
b) the statements $b = a$ and $a = b$ shall be interchangeable
c) from $a = b$ and $b = c$ must follow $a = c$
d) $a = a$ if K contains no other symbol equal to a.

2. *Definition.* An infinite set of symbols is one which contains parts that can be put into one correspondence with the whole. A finite set is one that is not infinite.

3. *Definition.* An ordered set is one in which we are always able to say either that a precedes b $(a < b)$ or that a follows b $(a > b)$ subject only to the restrictions that
a) the result of comparison is uniquely determined
b) $a < b$ shall exclude $a = b$ but involve $b > a$
c) if $a < b$ and $b < c$, then $a < c$
d) if $a' = a$ and $b' = b$, then $a' < b'$ or $a' > b'$ according as $a < b$ or $a > b$.

4. *Definition.* An ordered set is said to be well ordered when it has a first element and every subset beginning with the first element has an immediate successor in the given set.

5. *Definition.* A procedure whereby to every a, b of a K-class is assigned a definite symbol $c = a \circ b$ will be called a C-rule or rule of combination provided that by this assignment equals with equals give equals.

6. *Definition.* A K-class is said to possess the fundamental group property with respect to a C-rule when $a \circ b$ also belongs to K.

7. *Definition.* Modulus of a K-class with regard to a C-rule is a symbol u of K such that $a \circ u = a = u \circ a$ for every a in K.

8. *Proposition I.* An ordered set defined by the requirements: **a**) it shall contain a given symbol e; **b**) it shall possess the group property for every combi-

nation $e \circ a$ where a denotes a previously defined member of the set is also well ordered, infinite and forms a K-class with respect to the given rule. *Proof:* By hypothesis the set is to contain $e \circ e = e'$, $e \circ e' = e''$, $e \circ e'' = e'''$, . . . Since it is to be an ordered set no two of its members can be equal ∴ to every element of the whole set can be assigned some one of the subset e', e''', e^{v}, . . . That is, the set is infinite. And by **b**) every element has an immediate successor. Finally we have a test for equality which satisfies the requirements of § 1.

9. *Scholium.* A set defined as in § 8 contains no modulus. In what follows it will be referred to as an e-set.

10. *Postulates.* We postulate an e-set for a lower rule of combination which shall contain a lower symbol u and e-sets for both this and a higher rule which shall both contain a higher symbol w, the definitions of the rules of combination to be completed in §§ 17, 26, 28, 30.

11. The different sets $K[u \circ]$, $K[w \circ]$, $K[w \square]$ are to be so ordered that the lower shall precede the higher. Thus they form together a well ordered set

u, $u \circ u = u'$, $u \circ u' = u''$, $u \circ u'' = u'''$, ...
w, $w \circ w = wu'$, $w \circ wu' = wu''$, $w \circ wu'' = wu'''$, . . .
$w \square w = w^{u'}$, $w \square w^{u'} = w^{u''}$, $w \square w^{u''} = w^{u'''}$, . . .

12. *Postulates.* We postulate e-sets for the lower rule which shall contain respectively each of the symbols $w^{u'}$, $w^{u''}$, $w^{u'''}$, . . . in succession. Thus corresponding to every a of the set $K[w \square]$ we shall have an e-set $K[a \circ] : a$, $a \circ a = au'$, $a \circ au' = au''$, . . . Now taking *e. g.* $a = w^{u'''}$, by the principle of § 11 every member of $K[w^{u'''} \circ]$ precedes $ww^{u'''} = w^{u^{iv}}$ and therefore falls between $w^{u'''}$ and $w^{u^{iv}}$. That is, all these new e-sets are interpolated between successive

elements of $K[w\square]$. Hence the totality of symbols forms a well ordered set.

13. *Proposition II.* A rule of combination is associative throughout a given K-class if

$$a\circ(b\circ c)=a\circ b\circ c$$

for every a, b, c in K.

14. *Definition.* A K-class is said to form a semigroup with regard to a C-rule associative throughout K if by this rule unequals with equals always give unequals or if from the relation $a'\circ b=a\circ b$, resp. $a\circ b'=a\circ b$ we can always infer $a'=a$ resp. $b'=b$.

15. *Proposition III.* No semigroup contains more than one modulus for its defining C-rule. For if u and u' not $=u$ were both moduli, we should have $a\circ u'=a=a\circ u$ contrary to § 14.

16. *Definition.* An abelian K-class with reference to a C-rule is one for which the rule is without exception commutative.

17. *Proposition IV.* Sufficient conditions of an abelian class are the relations

$$a\circ(b\circ c)=a\circ b\circ c \quad\text{and}\quad b\circ a=a\circ b$$

for every a, b, c in the class.

18. *Proposition V.* A C-rule is distributive over another in a given K-class if the relations

$$(a\circ b)c=ac\circ bc \quad\text{and}\quad a(b\circ c)=ab\circ ac$$

are satisfied by every a, b, c in K.

19. *Proposition VI.* A necessary and sufficient condition of the generating rule of an e-set being associative for the set is the inductive formula of definition.

$$e\circ a\circ b=e\circ(a\circ b).$$

Proof. If the relation of $a\circ(b\circ c)=a\circ b\circ c$ has been established for a certain a and every b, c of the set, then by hypothesis $e\circ a\circ(b\circ c)=e\circ\{a\circ(b\circ c)\}=e\circ\{a\circ b\circ c\}=e\circ(a\circ b)\circ c=e\circ a\circ b\circ c$.

But $e\circ b\circ c = e\circ(b\circ c)$ by definition.

Therefore $e'\circ b\circ c = e'\circ(b\circ c)$ and so on.

Hence the theorem by strict induction.

20. *Corollary.* The rule is also commutative. For if $e\circ a = a\circ e$, then by the associative law $e\circ a\circ e = e\circ(a\circ e) = e\circ(e\circ a)$. But $e\circ e' = e'\circ e$ by § 19, therefore $e\circ e'' = e''\circ e$, and so on. And if $b\circ a = a\circ b$ for a certain a and every b then $b\circ(e\circ a) = b\circ(a\circ e) = b\circ a\circ e = a\circ b\circ e = e\circ(a\circ b) = e\circ a\circ b$.

Hence the proposition follows by strict induction.

21. *Proposition VII.* The formula of § 19 is also a sufficient condition of the e-set constituting an abelian semigroup for its generating C-rule. *Proof.* If $a\circ b$ belongs to the given e-set, then $e\circ a\circ b = e\circ(a\circ b)$ also belongs to it. Thus the first group property is established. We have proved the associative law and by definition no two numbers of the set are equal. Therefore $a'\circ b$ is not $= a\circ b$ when a' is not $= a$.

22. *Postulates.* Using capital letters $M, N, \ldots$ to denote elements of the lowest class K[$u\circ$], and italic letters $a, b, \ldots$ for those of the class K[$w\square$] where a shall precede b, we postulate for every $MB = BM$ a set $MB\circ Na$ for every Na, then using letters a, b, ... where a shall precede b to denote the resulting symbols we postulate inductively new sets $\mathrm{b}\circ\mathrm{a}$ where $\mathrm{a} = Na$ and b denotes successively the higher "polynomial" or composite symbols. Every b-set is to be simply ordered and possess the first group property for every $\mathrm{b}\circ\mathrm{a}$.

23. *Proposition VIII.* Every b-set is well ordered, infinite and forms a K-class for the rule denoted by $\circ$. For the b-set consists of the combinations b, $\mathrm{b}\circ\mathrm{a}$, $\mathrm{b}\circ\mathrm{a}\,u'$, $\mathrm{b}\circ\mathrm{a}\,u''$, $\mathrm{b}\circ\mathrm{a}\,u'''$, ... and the reasoning of *Prop. I* holds good.

24. *Proposition IX.* The b-sets belonging to a

given Mb form together an infinite, well ordered K-class as regards the rule $\circ$. For the set of b's:

$$Mb,\ Mb \circ w^{(n)},\ Mb \circ w^{(n \circ u)},\ \ldots .$$

forms a well ordered K-class between consecutive members of which the b-sets are interpolated.

25. *Proposition X.* The totality of the b-sets forms an infinite, well ordered K-class as regards the rule $\circ$. For the set of Mb belonging to a given b is a well ordered K-class and so is the whole set of b's, the latter being simply $K[w\square]$.

26. New combinations of symbols already defined are defined inductively in accordance with the formulas

$$b \circ a = a \circ b \quad \text{and}$$
$$a \circ (b \circ c) = a \circ b \circ c.$$

This secures the group property for the whole set and the reasoning of *VI* and *VII* establishes

Proposition XI. The set of symbols generated according to two rules, a higher and a lower, from a single arbitrary symbol w by aid of the postulate of order, the restricted form of the group property and the above inducted formulas of definition, is a well ordered, infinite set constituting an abelian semigroup with regard to the lower rule.

27. *Scholium.* The higher rule remains unrestricted and has not been defined beyond the set $K[w\square]$, therefore is not yet a C-rule for the K-class of § 26.

28. *Definition.* The higher rule shall be defined inductively throughout $K[w\square]$ by the formula

$$w\,a\,b = w \square a\,b,$$

where a, b are any members of $K[w\square]$ for which $a\,b$ has already been defined.

29. *Proposition XII.* The class $K[w\square]$ forms an abelian semigroup with regard to its generating rule. Proof by *Propositions VI* and *VII.*

30. *Definition.* The higher rule shall be defined inductively for the remaining symbols of our abelian semigroup on the lower rule according to the formulas

$$(a\circ b)c = ac\circ bc \text{ and } a(b\circ c) = ab\circ ac,$$

where the combinations ab, ac, bc shall have been already defined.

31. *Proposition XIII.* The higher rule is distributive over the lower throughout the class of symbols defined in § 22. *Proof.* First let $a = b = c = l$ where l is any symbol of $\mathrm{K}[w\,\square]$. Then ll is defined by § 28 and $l(l\circ l) = ll\circ ll = (l\circ l)l$ by § 30. Now suppose that the formulas of § 30 have been established for all symbols of $\mathrm{K}[l\circ]$ up to and including a certain a and for every b and c.

$$\begin{aligned}\text{Then } (l\circ a\circ b)c &= \{l\circ(a\circ b)\}c && \text{by associative law,}\\ &= lc\circ(a\circ b)c && \text{by hypothesis,}\\ &= lc\circ(ac\circ bc) && \text{by hypothesis,}\\ &= lc\circ ac\circ bc && \text{by associative law,}\\ &= (l\circ a)c\circ bc.\end{aligned}$$

Similarly in every other case when a, b, c are replaced by $l\circ a$, $l\circ b$, $l\circ c$ respectively. But by definition $l(l\circ \mathrm{N}a.) = ll\circ a\,\square\,\mathrm{N}a$ and so on. Therefore by strict induction the formulas hold for every a, b, c belonging to the same $\mathrm{K}[l\circ]$. Hence by *Prop. V* the theorem is true in this case. If h, k, l denote different members of $\mathrm{K}[w\,\square]$ the definition gives

$$(h\circ k)l = hl\circ kl \text{ and } h(k\circ l) = hk\circ hl.$$

Then the proof is completed inductively by the same reasoning as above.

32. *Corollary 1.* The higher rule is a C-rule and by it unequals with equals give unequals. For since our symbols form a well ordered set according to the lower rule, we have $\mathrm{a} = \mathrm{b}\circ\mathrm{x}$ for any two unequal elements a, b and therefore $\mathrm{ac} = \mathrm{bc}\circ\mathrm{xc}$ ∴ not $= \mathrm{bc}$.

33. *Corollary 2.* The higher rule is associative.

For this property has been established for the elements a, b, ... as members of $K[w\,\square]$. Therefore by the distributive law it holds generally.

34. *Corollary 3.* The higher rule is commutative. For this also has been proved in the class $K[w\,\square]$.

35. *Corollary 4.* The set of symbols defined in § 22 forms an abelian semigroup with reference to the higher rule.

36. *Scholium.* Beginning with any $a > w$ we have abelian semigroups with regard to both rules, and so beginning with w for one or the other rule, but no part beginning with w forms a semigroup on both rules.

37. *Proposition XIV.* Necessary and sufficient conditions that a set M constitute an abelian semigroup with respect to each of two rules of combination, one distributive over the other, that M contain an arbitrary w and that M be as generated an ordered set, are the rules of combination thus far defined.

38. *Corollary.* The properties in question may be expressed by the following postulates:

A. There shall be a higher and a lower rule of combination.

B. Combinations of symbols shall be so ordered that those made by the lower rule precede combinations of the same symbols by the higher.

C. The higher rule shall be distributive over the lower.

D. There shall be a set M containing the symbol w.

E. M shall form an abelian semigroup for the lower rule.

F. M shall form an abelian semigroup for the higher rule.

G. Every successive set generated according to requirements shall be an ordered set.

39. *Scholium.* M is a well ordered set with no modulus.

40. We postulated two rules of combination for the symbol w, but only one for the lower symbol u. If we should postulate a higher rule for u by the same requirements as for w the resulting set of symbols would not differ as regards any group property from the w-set; the new abelian semigroups would be respectively holoedrically isomorphic with the former. If we postulate no higher rule the set $K[u\circ]$ still forms an abelian semigroup holoedrically isomorphic with $K[w\circ]$.

41. Instead let us set up postulates for the u class of symbols differing from those of § 38 only in adding another postulate H. The symbol u shall be a modulus for the higher rule, with the restriction on A–G that they shall not conflict with H. Then the class $K[u\square]$ reduces to the single element u, the abelian semigroup on the two rules reduces to the set $K[u\circ]$ and postulate B drops out, since every combination by the higher rule is found among those made according to the lower rule. This new set of postulates may be replaced by the equivalent set.

42. **a.** There shall be a higher rule defined from a lower by the inductive formulas $(u\circ a)b = ub\circ ab$ and $a(u\circ b) = au\circ ab$.

b. There shall be a lower rule defined inductively by the formula $u\circ a\circ b = u\circ(a\circ b)$.

c. There shall be a set M containing the symbol u.

d. The set M shall possess the group property for every combination $u\circ a$.

e. M shall be an ordered set.

f. There shall be a set M′ built up by postulates c, d and e on the symbol uu.

g. The sets M′ and M shall be identical.

43. *Proposition XV.* The set of symbols defined by the above seven postulates constitutes an abelian semigroup for each rule and has a modulus for the higher rule, which is distributive over the lower.

Proof. The abelian semigroup on the lower rule is established by *Prop. VII,* the distributive law follows from XIII and the other semigroup by § 35. It remains to prove the existence of a modulus.

Let $e = uu$. By postulate g, e must occur in the set $K[u\circ] : u, u', u''$, . . .

Suppose $e = u''$. Then every member of $K[e\circ]$ will be found in $K[u\circ]$ but beyond u'. That is, u and u' are not in $K[e\circ]$, contrary to g. Therefore the only possibility of satisfying g is $e = u$. Since, then, $uu = u$, it follows by the distributive law that u is a modulus.

44. Postulates a . . . g define the natural numbers as ordinal symbols and by *XV* contain all the laws of their arithmetic. The cardinal numbers may be defined in a manner now familiar as names of classes, *e. g.,* "five" is the name given to the class of all well ordered sets which are ordinally similar to the set u, u', u'', u''', u^{iv}.

45. *Definition.* A group is a semigroup which contains, corresponding to every a, b, in it, symbols p and q such that $a\circ p = b = q\circ a$.

46. *Proposition XVI.* Every group contains a modulus with respect to its defining C-rule.

47. *Definition.* If a class which has a modulus u for its defining C-rule contains symbols a, $\bar{a}$ such that $a\circ\bar{a} = u = \bar{a}\circ a$ then a, $\bar{a}$ are said to be each the *inverse* of the other.

48. *Proposition XVII.* No member of a semigroup can have more than one inverse in the semigroup. For otherwise equals with unequals would give equals.

49. *Proposition XVIII.* Every group contains the inverse of every one of its members.

50. *Proposition XIX.* A semigroup with modulus is a group if it also contains the inverse of every one of its members.

Proof. $a \circ (\bar{a} \circ b) = a \circ \bar{a} \circ b = u \circ b = b$, and $(b \circ \bar{a}) \circ a = b \circ (\bar{a} \circ a) = b \circ u = b$, that is, § 45 is satisfied by $p = \bar{a} \circ b$ and $q = b \circ \bar{a}$.

51. *Proposition XX.* Given an abelian semigroup G with reference to a rule denoted by $\circ$, if in the class $[(m, n)] = \mathrm{C}$ of pairs of elements of G we declare $(m, q) = (n, p)$ when and only when $m \circ p = n \circ q$ and set up a rule defined by the relation $(m, q) \odot (n, r) = (m \circ n, q \circ r)$, then 1) C will be a K-class, 2) $\odot$ a C-rule, 3) C an abelian group as regards the rule denoted by the sign $\odot$.

Proof. 1) Either $m \circ p = n \circ q$ or $m \circ p$ is not $= n \circ q$ by hypothesis and § 1. Hence either $(m, q) = (n, p)$ or (m, q) is not $= (n, p)$. Obviously the assertions $(n, p) = (m, q)$ and $(m, q) = (n, p)$ are identical in meaning, since this is so for $n \circ q$ and $m \circ p$. It remains to verify the euclidean postulate.

Suppose that $(m, q) = (l, r)$ and $(l, r) = (n, p)$.
Then $m \circ r = l \circ q$ and $l \circ p = n \circ r$.
Hence $(m \circ r) \circ (l \circ p) = (n \circ r) \circ (l \circ q)$.

But since G is an abelian semigroup $(m \circ r) \circ (l \circ p) = m \circ r \circ l \circ p = (m \circ p) \circ (l \circ r)$ and likewise $(n \circ r) \circ (l \circ q) = (n \circ q) \circ (l \circ r)$. Therefore $(m \circ p) \circ (l \circ r) = (n \circ q) \circ (l \circ r)$. Whence $m \circ p = n \circ q$ by definition of semigroup and finally $(m, q) = (n, p)$ by definition of equality.

2) Let $(m', q') = (m, q)$ and $(n', r') = (n, r)$. Therefore $m' \circ q = m \circ q'$ and $n' \circ r = n \circ r'$. Whence as under 1) $(m' \circ n') \circ (q \circ r) = (m \circ n) \circ (q' \circ r')$ and hence $(m' \circ n', q' \circ r' = (m \circ n, q \circ r)$. That is $(m', q') \odot$

$(n', r') = (m, q) \odot (n, r)$, or equals by equals give equals and $\odot$ denotes a C-rule.

3) The fundamental group property is secured by the definition. To prove the associative law we have $(m, n) \odot \{ (p, q) \odot (r, s) \} = (m \circ p \circ r, n \circ q \circ s) = (m, n) \odot (p, q) \odot (r, s)$. Suppose that $(m', q') \odot (n, r) = (m, q) \odot (n, r)$. Then $(m' \circ n, q' \circ r') = (m \circ n, q \circ r)$ by definition. Hence $(m' \circ n) \circ (q \circ r) = (m \circ n) \circ (q' \circ r)$ and $(m' \circ q) \circ (n \circ r) = (m \circ q') \circ (n \circ r)$. Therefore $m' \circ q = m \circ q'$ by § 14. That is $(m', q') = (m, q)$ and similarly for the other form of this property. Thus C is a semigroup. But the element (m, m) is a modulus and to every (n, q) corresponds an inverse (q, n). Therefore by *XIX*, C is a group, which we will denote by G.

$$\text{Finally } \quad (n, r) \odot (m, q) = (n \circ m, r \circ q)$$
$$= (m \circ n, q \circ r) = (m, q) \odot (n, r).$$

Therefore by § 16, G is an abelian group.

52. The semigroup C and group G are connected by *Proposition XXI.* If we declare $(m \circ q, q) = m$ then $(m \circ q, q) \odot (n \circ r, r) = m \circ n$. For $(m \circ q, q) \odot (n \circ r, r) = (\overline{m \circ q} \circ \overline{n \circ r}, q \circ r) = m \circ n \circ q \circ r, q \circ r) = m \circ n$.

53. *Scholium.* The group G contains a semigroup K holoedrically isomorphic with C in such manner that the rule $\odot$ becomes identical with the rule $\circ$ for K.

54. Obviously *Prop. XX* may be applied to the set of natural numbers in two different ways according as we use the semigroup on addition or that on multiplication. An essential distinction between these two procedures is furnished by

55. *Proposition XXII.* Given two rules of combination of which one is distributive over the other, no set of symbols can form a group with respect to both rules. For such a set would contain a modulus v for the lower rule (*XVI*). Then by the distributive law

$a = bx = b(x \circ v) = bx \circ bv = a \circ bv$ for every a. That is bv is also a modulus. But there can not be more than one modulus (*III*). Therefore $bv = v$ for every b so that when b' is not $= b$ we have $b'v = v = bv$ contrary to definition.

56. *Corollary.* It is not possible to define a set of symbols constituting a semigroup with modulus as regards both rules of § 55.

57. If *Prop. XX* is applied to the set of natural numbers and the rule of addition, we lose the semigroup on multiplication and can not recover it. This semigroup, in fact, is destroyed if we only annex a modulus for addition. Consequently we give the preference to the semigroup on multiplication and proceed with the group G obtained by applying *XX* to it.

58. *Proposition XXIII.* Given a higher rule distributive over a lower, and a set of symbols forming an abelian semigroup with respect to each rule, if we build the group G of § 52 with reference to the higher rule, then a necessary and sufficient condition of having a lower rule over which the higher shall be distributive and with regard to which G shall constitute an abelian semigroup is the formula of definition $(m, q) \circ (n, r) = (mr \circ nq, qr)$.

Proof. The necessity of this relation is obvious. To show that it is sufficient we first let $(m', q') = (m, q)$ and $(n', r') = (n, r) \therefore (m'q = mq')$ and $n'r = nr'$. Therefore $m'r'qr = m'qrr' = mrq'r'$ and $n'q'qr = nqq'r'$. Hence $(m'r' \circ n'q)qr = (mr \circ nq)q'r'$ by distributive law and $\therefore$ by definition $(m'r' \circ n'q'q'r') = (mr \circ nq, qr)$ or equals with equals give equals and we have a C-rule. Similarly equals with unequals give unequals. For the associative law $(k, l) \circ \{(m, q) \circ (n, r)\} = (k, l) \circ (mr \circ nq, qr) = (kqr \circ lmr \circ lnq, lqr) = (kq \circ lm, lq) \circ (n, r) = (k, l) \circ (m, q) \circ (n, r)$.

Obviously $(n, r) \circ (m, q) = (m, q) \circ (n, r)$. Thus we have an abelian semigroup and the distributive principle follows by taking equals with equals.

59. *Definition.* The symbols of G shall be ordered according to the convention that (m, q) shall precede or follow (n, q) according as m precedes or follows n and by § 3.

60. *Scholium.* If a, b denote two natural numbers that have no common factor other than unity, the set of symbols (a, b) is simply ordered by the above definition. This set, which we will denote by R, may be taken as representative of G since every element of G is equal to some member of R.

61. *Definition.* The symbols constituting the set R are called absolute, rational numbers.

62. *Proposition XXIV.* Every two unequal elements of G are connected by a relation $h = g \circ x$ where h, g denote the given elements, g being that which precedes.

For $g = (m, q) = (mr, qr)$ and $h = (n, r) = (nq, qr)$ and mr precedes nq by hypothesis. Therefore $h = g \circ x$ is satisfied by $x = (d, qr)$ where $nq = mr \circ d$.

63. *Corollary.* The set R is simply ordered according to the lower rule denoted by $\circ$.

64. *Proposition XXV.* If we exclude the modulus u the remaining symbols of R form a set which is simply ordered according to the higher rule. For let x denote any element of R which precedes and y any one which follows u.

Then gx precedes and gy follows g. That is, the trios u, g, gx and u, g, gy are ordered whether g precedes or follows u.

65. *Corollary.* The modulus u separates the remaining symbols of R into two simply ordered classes, neither of which contains either a first or last element.

66. It is possible to divide R into two ordered classes so that every element of R belongs either to the one or to the other, but neither class has either a first or a last member. For example, the class R_1 of all elements whose squares precede 2 and the class R_2 of all whose squares follow 2 together exhaust the set R, while neither R_1 nor R_2 has either a first or a last element. If we take 4 instead of 2, the element 2 is not included either in R or in R_2; it separates them. We usually make this separation in practice by selecting a well ordered set, *e. g.* according to the decimal scale. We take first the highest integer in R_1, then the highest number of tenths, hundredths and so on. Similarly we pick out first the lowest integer in R_2, then the lowest set of tenths, hundredths, etc.

67. *Definition.* A well ordered set which has no last element is called a series.

68. *Definition.* The series of all symbols of the well ordered set $1, 2, \ldots w, w+1, \ldots 2w, \ldots 3w, \ldots w^2, \ldots$ which precede the element a taken in the above order, is said to be a series of type a.

69. *Definition.* An ordered set which has no first nor last element will be called an unbounded set.

70. Given an unbounded set S ordered according to a rule with respect to which S constitutes an abelian semigroup, suppose that a series $K[f_n]$ of type w has been selected from among the elements of S and let W_1 denote the set of all symbols of S which follow, V_2 all which precede every f_i, let V_1 denote the set of all symbols s which precede W_1 and W_2 the set of all that follow V_2.

Then one of the sets W_1, V_1 must be unbounded and both may be. So also of V_2 and W_2.

71. In every one of the four cases when
W_1 has a first element or V_1 has a last
V_2 has a last element or W_2 a first
this element is called the limit of the set to which it belongs.

72. In case W_1 and V_1 or V_2 and W_2 are both unbounded we will introduce a new symbol f_w which we will call the limit of $\mathrm{K}[\mathrm{f}_n]$.

73. *Lemma.* If W_i and V_i are both unbounded for the series $K[\mathrm{f}_n]$ the same is true for the series $K[a \circ \mathrm{f}_n]$ where a is any symbol in S. For if either the W or V set corresponding to $K[a \circ \mathrm{f}_n]$ had a limit l we could write $l = a \circ x$ and x would be a limit for the same W or V belonging to $\mathrm{K}[\mathrm{f}_n]$ contrary to hypothesis.

74. *Theorem.* If the series $K[\mathrm{f}_i]$, $K[\mathrm{g}_j]$ both divide S into two unbounded sets the same is true of the set $K[\mathrm{f}_i \circ \mathrm{g}_i]$.

Proof. Let $\mathrm{h}_1 = \mathrm{f}_1 \circ \mathrm{g}_1$, $\mathrm{h}_2 = \mathrm{f}_2 \circ \mathrm{g}_2$, ...
$\mathrm{h}_{w+1} = \mathrm{f}_2 \circ \mathrm{g}_1$, $\mathrm{h}_{w+2} = \mathrm{f}_2 \circ \mathrm{g}_2$, . . .
$\mathrm{h}_{2w+1} = \mathrm{f}_3 \circ \mathrm{g}_1$, $\mathrm{h}_{2w+2} = \mathrm{f}_3 \circ \mathrm{g}_2$, . . .

Then by the Lemma each of the series $\mathrm{K}[\mathrm{h}_j]$, $\mathrm{K}[\mathrm{h}_{w+j}]$, $\mathrm{K}[\mathrm{h}_{2w+j}]$, . . . $\mathrm{K}[\mathrm{h}_{iw+j}]$, . . . divides S into two unbounded sets. Hence the same is true of the set h_1, h_{w+2}, h_{2w+3}, . . . h_{iw+i+1}.

75. On the basis of the preceding theorem and definitions is built up, by laying down the usual definitions of equality, order and two rules of combination, the set X of limits of series $\mathrm{K}[\mathrm{f}_n]$ selected out of R. The set X forms an abelian group with reference to the higher rule of combination and an abelian semigroup on the lower rule. The higher rule is distributive over the lower and possesses the modulus u. X may be simply ordered according to the lower rule and is divided by the modulus u into two unbounded sets each

simply ordered according to the higher rule. X is itself an unbounded set and contains a sub set holoedrically isomorphic with R as regards each rule of combination. Thus the whole set of absolute numbers is deduced from the set of absolute rational numbers by using only principles of order.

76. The preceding development does not take account of the possibility that $K[f_n]$ may not really divide S. There may be no symbol which follows every f_i. Then W_1 is an empty class and V_1 is taken to coincide with S. Thus if $K[f_n]$ and $K[g_n]$ are both series of this kind, they both have the same W and V, whence if new symbols f_w, g_w were to be introduced the principle of definition used in § 75 would lead us to declare $f_w = g_w$. Therefore we assign to the totality of the sets $K[f_n]$ for which W_1 is an empty class a single symbol Z which is to follow every element of X. Then following § 75, $Z \circ g_w$ is to be defined as h_w where $h_n = f_n \circ g_n$ and $f_w = Z$. But for $K[h_w]$, W_1 is empty, therefore $Z \circ x = Z \circ g_w = h_w = Z$. That is, $Z + x = Z = x + Z$, $Zx = Z = xZ$, and similarly $Z + Z = Z = ZZ = Z^3 = Z^N$. The associative, commutative and distributive laws still hold as well as the first group property, but the semigroup is destroyed for both rules by violating the law of equals with unequals.

77. It is also possible that no symbol in S precedes every f_i. Then V_2 is an empty class and W_2 coincides with S. On the same principle as in § 76 we assign to the totality of series of this kind a single symbol v to precede every x and define $v \circ x = h_w$ where $h_n = f_n \circ g_n$, $g_w = x$, $f_w = v$. And now the two rules must be distinguished. Since no x precedes every f_i the sets $K[f_n + g_n]$ and $K[g_n]$ separate S into the same V and W. Therefore $v + x = h_w = g_w = x + v$. And for the same reason no s can precede every $f_n\, g_n$

$$\therefore \quad vx = (fg)_w = v = xv$$

Also in like manner $\mathrm{v} + \mathrm{v} = \mathrm{v} = \mathrm{vv}$.

In the set K[h, v] the associative, commutative and distributive laws and the first group property are all preserved. The law of equals with unequals is violated for multiplication but still holds for addition, for which v is a modulus.

78. Since the introduction of infinity would destroy both semigroups while zero destroys only that on multiplication, it seems preferable to admit zero to our arithmetic and exclude infinity. But this removes the only objection to enlarging the addition semigroup into a group. This is effected at a stroke by applying *Prop. XX* to the set *X* and thus building an abelian group with reference to addition. In this group we then define a higher rule by the formulas

$$\overline{a} \odot b = \overline{ab} = a \odot \overline{b} \quad \text{and} \quad \overline{a} \odot \overline{b} = ab\,.$$

This completes the system of real numbers, forming an abelian group on addition and, when we exclude its modulus, an abelian group on multiplication, which is distributive over addition. The system of real numbers can be simply ordered according to the lower rule, but the abelian group on the higher rule can not be similarly treated.

79. We might have proceeded by first applying *XX* to the natural numbers as a semigroup on addition. This yields the whole set of integers, positive, negative and zero. Omitting zero and defining by the law of signs we should have an abelian semigroup on multiplication. Applying *XX* to it, there results an abelian group composed of all rational numbers except zero. Then the introduction of the limits would supply the whole set of irrational numbers and close by reintroducing zero.

80. As long as we postulate two rules of combination, one distributive over the other, and demand semi-

groups with reference to both, we are led inevitably to the transfinite types in case we impose no restriction on the multiplication table and, if we require a modulus, to the natural numbers, whence the system of real numbers results from the attempt to build groups. The two rules of combination connected by the distributive property may be regarded as defining arithmetic up to date; it has not yet been found profitable to postulate in any other way. Then transfinite arithmetic is distinguished by postulating the semigroups and finite arithmetic by the postulate of the modulus.

81. The real numbers form the most general finite system with a single unit and must enter into every system with more than one principal unit, one unit must always be the modulus. Systems with two or more principal units have been studied exhaustively by Weierstrass. Here the abelian group on the lower rule is postulated universally.

With two principal units, if we exclude the modulus of the lower rule, the necessary and sufficient condition of an abelian semigroup on the higher rule is the existence in the system of a symbol i such that $ii = \bar{u}$. Thus the common complex numbers form the most general system with two principal units satisfying the postulates for real members.

82. Within the system of common algebra are distinguished different number bodies each built on a root of a given algebraic equation as a unit. The algebraic numbers of a given body form an abelian group on addition and, excluding zero, an abelian group on multiplication, and must contain a given symbol, the root of the given algebraic equation. For example the system of common complex numbers is the number body which contains a root of the quadratic $x^2 + 1 = 0$.

83. An integral algebraic number satisfies an equation

$$x^N + a_1 x^{N-1} + \ldots + a_i x^{N-i} + \ldots + a_n = 0,$$

where every a_i is an integer. A good illustration of the serviceableness of the group theory process for arithmetic is the theorem: The whole numbers of a quadratic number body form an abelian group on addition and, if we exclude zero, an abelian semigroup with regard to multiplication.

84. A more striking illustration is furnished by Dedekinds' "Ideals." An ideal is defined as a combination of the whole numbers of a number body possessing the first group property for both addition and multiplication. The ideals of a given body form an abelian semigroup with respect to multiplication. There is no addition of ideals.

85. Similar applications are found in the expression of an ideal by aid of its basis and in the cognate formulation of the transformations of a collineation in space of N dimensions. The latter question resolves itself into that of complex numbers with N principal units. Here it is no longer possible to preserve even the restricted abelian semigroup on the higher rule.

Not only is the abelian character lost, as in quaternions, but the semigroup property may be violated on account of the possibility of a combination by the higher rule being zero when none of the factors is zero.

86. It is now possible to describe more concisely the relation of the transfinite arithmetic to common arithmetic. The symbols defined in § 22 form a set of numbers with infinitely many principal units w, w^2, w^3, . . *i. e.*, the principal units form a series of type w. In finite arithmetic, it is true, the symbols u^2, u^3, . . . all belong to the set generated from u as principal unit, but if we allow this analogy in the transfinite system there will be still more new symbols.

For just as the removal of restrictions on the higher rule carried our series of symbols beyond the finite set of type w so the introduction of a still higher rule, corresponding to involution, will extend it beyond the set defined in § 22 if we impose no restrictions on the new rule except that of order and the special form of the group property.

87. Let us postulate a rule expressed by a^b higher than the two preceding, that is, the combination a b shall precede a^b. To distinguish we will now call $a b$ the lower and $a \circ b$ the lowest rule.

The lower rule has been shown to be associative and commutative for the set $K[w \square]$, which forms an abelian semigroup with regard to it. A set of symbols shall be generated from w by the higher rule in accordance with the postulate of order and the restricted form of the group property for w^a, where a is a previously defined element. By Prop. I this set forms a series $w, w^w = w', w^{w'} = w'', w^{w''} w''', \ldots$ and now w' must follow every w^N $(N = 2, 3, \ldots)$ [w^N is not a combination by rule, the N is a mere index]. Then by § 22 we obtain a series holoedrically isomorphic with the set there considered if to the lowest and lower rules respectively we make the lower and higher correspond.

88. The articulation of the two lower rules in §§ 28–35 leaves room for much freedom in definition. There we defined the lowest rule first and made the lower depend upon it. Here we have already defined the lower rule to the extent implied in the application of § 22. This, however, involves no further restriction than the inductive associative formula of § 19. But the definition from the lowest rule carries this property with it.

It is therefore permissible to define the lowest rule so that the lower shall be distributive over it. Then by the process of § 22 new combinations are made by the higher and lowest rule together, from each series of type w in the present set of symbols a new set of the same type as that in § 22. And all new series being fitted in by the nature of the process between consecutive elements of the series previously defined we have at every stage a totality of symbols forming a series.

89. The group properties of the two lowest rules are preserved throughout the preceding process. On every new symbol not obtained from the preceding by postulating them is built up a set forming abelian semigroups on both the lower and lowest rules, the new symbol playing the part of a unit precisely like w in the series of § 22, and in this set the lower rule is distributive over the lowest. This process is to be continued as long as new symbols can be obtained by it.

90. There remains one more possibility of building new symbols by introducing a combination defined one way of the higher symbols with those of the series $\mathrm{K}[u \circ]$ according to the lowest rule. Thus to every a in the higher series will be assigned a w-series a, $\mathrm{a} \circ u$, $\mathrm{a} \circ u'$, $\mathrm{a} \circ u''$, $\mathrm{a} \circ u'''$, . . .

This series fits in between a and its next following element in the former set so that we still have a totality forming a series.

91. For completeness it is convenient also to define combinations one way of certain symbols with those of $\mathrm{K}[u \circ]$ according to the other two rules, viz.: those expressions in which the symbols of $\mathrm{K}[u \circ]$ have already been used as marks or indices, *e. g.:*

$u'w$, $u''w$, $u'''w$, . . . $w^{u'}$, $w^{u''}$, $w^{u'''}$, . . .
$u'w'$, $u''w'$, $u'''w'$, . . . $w'^{u'}$ $w'^{u''}$, $w'^{u'''}$, . . .

Expressions $u \circ a$, $u' \circ a$, . . . u'^{w}, u''^{w}, . . . $u'^{w'}$, $u''^{w'}$, . . . are not defined, neither are there any combinations according to the higher rule except the set w^{a} where a belongs to this set. The higher rule has not been made a rule of combination for any whole set. This would involve assigning properties to it and completing the arithmetic of the symbols we have defined, which is beyond the present purpose. It is enough to have them in series; that forms the foundation of their arithmetic.

92. The mere existence of the series of symbols developed in the preceding §§ is enough to solve a great variety of problems arising in analysis, the nature of which will be illustrated by comparing this series with series consisting of absolute numbers. The natural numbers form a series of type w if they are arranged in the order of their genesis. It is, however, possible to arrange them in series of higher types for *e. g.* the odd numbers alone form a series of type w. If to this we add on the even numbers successively we obtain series of types

$$w+1,\ w+2,\ \ldots\quad w+N,\ \ldots$$

and thus the whole set is ordered in type $2w$.

If we order the set R of § 60 as follows:

$$(1,1),\ (2,1),\ (3,1).\ (4,1),\ \ldots$$
$$(1,2),\ (3,2),\ (5,2),\ (7,2),\ \ldots$$
$$(1,3),\ (2,3),\ (5,3),\ (7,3),\ \ldots$$

we have a series which can be put ordinally into one to one correspondence with the series $1, 2, \ldots$ $w+1,\ w+2,\ \ldots\ 2w,\ 2w+1,\ \ldots$ *i. e.*, is of type w^2.

The same set of numbers (the common fractions) can, however, be arranged in a series of higher type. For every finite, simple, continued fraction is equal to some common fraction and conversely. Now let us order the finite continued fractions according to the values of their successive quotients

$$q_1,\ q_2,\ q_3,\ \ldots\ q_N.$$

Thus the continued fractions containing each a single quotient form a series of type w. Then from each member of this series by adding a second quotient results again type w. Therefore the fractions of the form $\frac{1}{q_1+}\,\frac{1}{q_2}$ may be arranged in series ordinally similar to $1, 2, \ldots w+1, \ldots 2w, \ldots 3w, \ldots$ *i. e.* of type w^2. Annexing a third quotient replaces each element of this set by a series of type w so that we include types $w^2+1,\ w^2+2, \ldots 2w^2, \ldots 3w^2, \ldots$ *i. e.* the class of fractions $\frac{1}{q_1+}\,\frac{1}{q_2+}\,\frac{1}{q_3}$ is ordered in type w^3.

Therefore the whole set of simple continued fractions, comprehending types $w, \ldots w^2, \ldots w^3, \ldots w^N, \ldots$ constitutes, as ordered, a series of type $w^w = w'$.

93. Now it is easy to arrange the natural numbers also in a series of type w' as follows. We know that the class of prime numbers can be put into one to one correspondence with the whole set of natural numbers (the number of primes is infinite).

Therefore we can set up a one to one correspondence ordinally between the prime numbers and the simple continued fractions with a single quotient. By the same reasoning the continued fractions with two quotients are shown to be ordinally similar to the class of product of two primes, *i. e.*, if to every quotient q_1 we assign that prime p_1 for which q_1 is the ordinal number in sequence (so that *e. g.* to the quotient 7 we assign 17) and likewise for a second prime p_2 and quotient q_2, and so on.

Proceeding in this way the class of all products of N primes is exhibited as ordinally similar to the class of continued fractions $\frac{1}{q_1+}\,\frac{1}{q_2+}\cdots\frac{1}{q_N}$. But the class of all products of primes is the whole set of natural numbers. Therefore by § 92 the natural numbers may be arranged in series w'. Q. E. D.

94. In other words we have here a method whereby

the elements of any w-series may be rearranged so as to produce a series of type w^w. Applying this method successively to the w-series in the preceding we obtain in place of w, $2w$, . . . w', $2w'$ . . . that is, instead of w^2 we get a type ww'. Then w^2+w, w^2+2w, . . . are replaced by $ww'+w'$, $ww'+2w'$, . . . making in all type $2ww'$ replacing the former $2w^2$.

Then come in succession types $3ww'$, $4ww'$, . . . so that the original w^3 expands into a type w^2w'. It is clear that in this way we retrace precisely the steps of the process of § 22, building up on each new symbol the abelian semigroups according to the lower and lowest rules.

Therefore by successive applications of the method it will be possible to rearrange the natural numbers in series of types as high as any of the set hitherto defined. This result may also be stated. The transfinite ordinal series so far defined may each be put into one to one correspondence with the set of natural numbers.

95. The symbols w, $w+1$, $w+2$, . . . *i. e.*, the transfinite symbols, are said to form the second ordinal class, the finite symbols constituting the first class. The latter class was said to be of type w, where w is the symbol following next after all the finite symbols of $K[u\circ]$. Likewise we shall say that the first and second ordinal classes together form a series of type W, introducing this new symbol without assigning to it any properties except that it shall follow next after all symbols of the second ordinal class, *i. e.*, after all the set $K[w^a] : w, w', w''$, . . .

96. We see that the ordinal symbols play a double role. They were defined as symbols forming a well ordered set. But to each symbol which has no immediate predecessor corresponds a series of which it is the type, viz.: the series of all its predecessors or any ordinally similar series. The arrangements of the nat-

ural numbers in § 94 are only a part of these series. But they are also only a part of the permutations of the whole set of natural numbers. Other permutations are obtained by the following *Lemma*. From any w series of symbols may be obtained a set of permutations of the symbols forming a series of type $w' = w^w$.

Proof. Let $a_1, a_2, \dots a_N, \dots$ denote the given symbols in the given order. Without changing the order of the higher a's put a_1 successively in every subsequent place. This set of permutations is obviously of type w.

From every one of them by repeating the process on a_2 we obtain again a w-series $\therefore$ in all a series of permutations of type w^2. Repeating the process with a_3, $a_4, \dots$ successively we have a series of permutations whose type is w'. Q. E. D.

97. Thus the arrangements of the natural numbers furnish a series of type not lower than W. For by § 96 we first deduce from the series 1, 2, 3, ... *i. e.*, the normal order, a set of permutations forming a series of type w'. That is, to every ordinal symbol preceding w' is assigned a permutation, and *vice versa*. Then by § 94 arrange the natural numbers in series w' which obviously is a different permutation from any of the preceding $\because$ it can not be obtained by the process of § 96. Now repeating the method of § 96 on each w-series of this permutation we use up all ordinal symbols between w' and that which results from it by a second application of § 94. This holds step by step as long as the latter process can be carried on. Thus to every ordinal symbol in succession preceding W is assigned a new permutation. That is, we have a set of permutations of all the natural numbers forming a series whose ordinal type is W.

98. The process just described for making permutations of all the natural numbers can not yield a series

of type higher than W since, as we have seen, it generates precisely the series W of ordinal symbols. That there are types higher than W is obvious, for we can proceed with W just as with w to generate new e-sets and new abelian semigroups, and there is no limit to the possibilities in the way of still higher symbols and rules. Now it is quite conceivable that there may be further permutations of natural numbers not obtainable by the above process. As a first step toward investigating this question let us consider the simpler one whether the natural numbers themselves can be arranged in a series of ordinal type higher than W. For this purpose we will establish the following

Lemma. Permutations of the natural numbers can be made by the process described and ordered so as to form a series of type higher than any series of all the natural numbers, however arranged. For by the process in question we can always form a new permutation which differs from the first permutation in at least its first element, from the second in at least its second element . . . . . . from the $(w+1)$st in at least its $(w+1)$st element, and so on, therefore is not included in any set of permutations ordinally similar to any possible arrangement of all the natural numbers. From this Lemma we readily obtain the

Theorem. Every possible arrangement of the natural numbers is a series of the second class. For by the Lemma to every such arrangement in series can be assigned a set of permutations forming a series of higher ordinal type. But by § 97 the process by which this is effected yields a set of permutations forming a series of type W. Therefore every possible arrangement of natural numbers in series is of type lower than W, therefore belongs to the second ordinal class (being *ipso facto* $\geq w$). Q. E. D.

99. The arrangement of the natural numbers in series of type higher than w finds application in the study of infinite continued fractions. By aid of the euclidean algorithm for greatest common divisor every absolute irrational number less than unity can be expressed as an infinite continued fraction

$$\frac{1}{q_1 +}\frac{1}{q_2 +} \cdot \cdot \cdot \cdot \frac{1}{q_N +} \cdot \cdot \cdot \cdot$$

and conversely. The class of infinite simple continued fractions may therefore be taken as the representative of the class of irrational numbers between zero and 1.

An infinite continued fraction can not be obtained from a finite one merely by annexing quotients; it can only be described by assigning a law which determines q_N for every value of N. An infinite continued fraction may be formed, *e. g.*, by the law that every quotient shall be 2. It is sufficient, however, to consider the class in which the quotients are all different; this can be put into one to one correspondence with the whole class. Accordingly we are concerned with the class of all possible permutations of all the natural numbers. These permutations may be examined in the same way as the permutations of a finite set by imagining a framework of places to be filled, but the number of places is infinite. Moreover, we must provide for the possibility of filling the places in a series of order higher than w. Thus an infinite continued fraction can be formed by filling the even places successively with the odd numbers in their natural order and the odd numbered places with even numbers in the same way, *i. e.*,

$$\frac{1}{2+}\frac{1}{1+}\frac{1}{4+}\frac{1}{3+}\frac{1}{6+}\frac{1}{5+} \cdot \cdot \cdot \cdot \cdot \cdot$$

or by filling the odd numbered places with primes and the even places with composite numbers. Or we can select first the places whose indices are primes, then the indices which are products of two primes, three primes, and so on, and fill these sets with the corresponding sets of numbers permuted in any way we please.

100. We have seen that every possible arrangement of all the natural numbers in a series is of type lower than W. Therefore the quotient places of our framework *in the order in which we propose to fill them* (or rather state how they shall be filled) constitute an ordinal type of the second class. That is, the *numbered places* in a permutation of all the natural numbers, arranged, however, *in the order in which they are to be filled*, form a series obtainable by the process of § 97.* Hence there can be no permutation of all the natural numbers not obtainable by this process, since such a permutation would be *eo ipso* different from all of those hitherto obtained and well ordered in some definite numbered places. In other words, this would mean that the series of the places as they are filled, or the series of numbers with which each place is to be filled, was not obtainable by the process of § 97. Therefore all possible permutations of the natural numbers form a series closely related to the series of type W.

BIOGRAPHY.

I, ARTHUR BOWES FRIZELL, member of the Protestant Episcopal Church, was born in Boston, July 14, 1865. My parents were Joseph Palmer Fessenden Frizell, civil and hydraulic engineer, and Julia Anna (Bowes) Frizell. My early education was chiefly at home and in a private school in Dorchester, Mass. I graduated from the high school in St. Paul, Minn., and spent three years at the Massachusetts Institute of Technology, where I afterwards served as assistant instructor in mathematics, 1888–'91. I received the degree of Bachelor of Arts from Harvard College in 1893 and that of Master of Arts from Harvard University in 1900. I served as instructor in mathematics at New York University 1895–'96, and at Harvard 1897–1906, when I resigned to study abroad. After three semesters at Göttingen, I returned to America, and was appointed, 1908, Professor of Mathematics in Midland College, Atchison, which position I resigned, 1909, to accept an instructorship in the University of Kansas.

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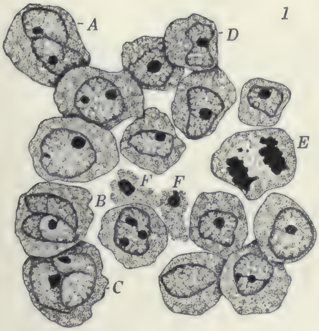
*And the preceding statements apply *verbatim* to every series of values admissible in a given numbered place.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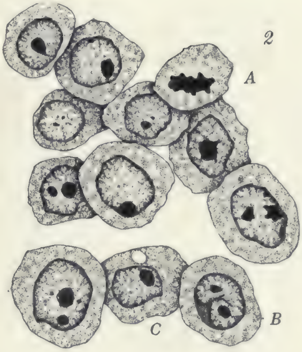
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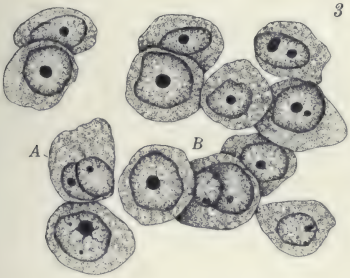
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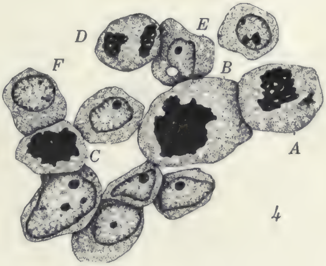
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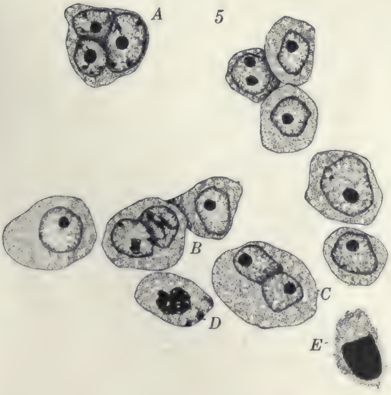
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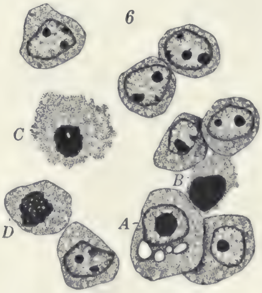
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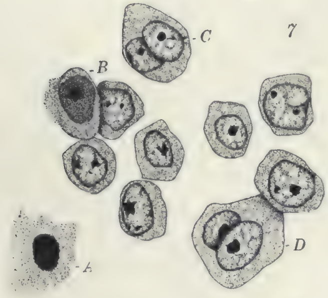

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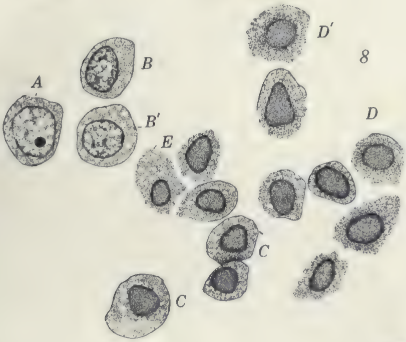

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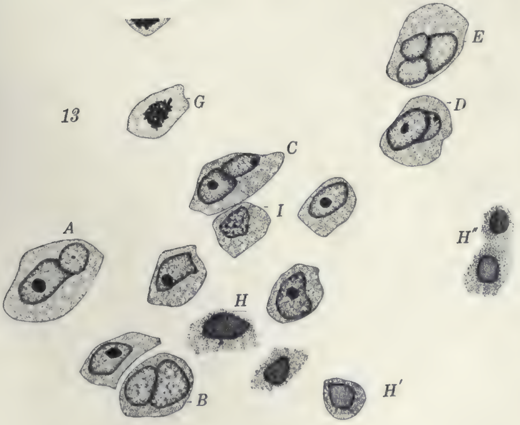
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B
H'

12

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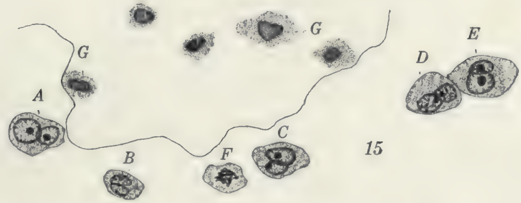

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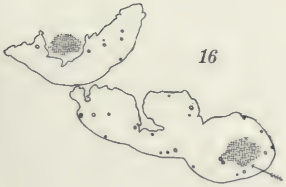

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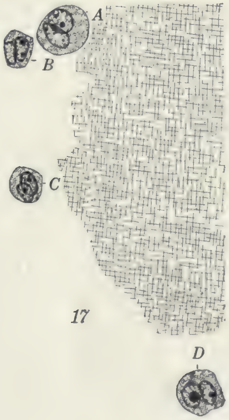

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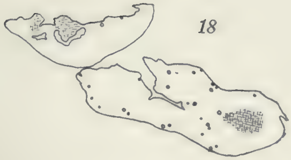

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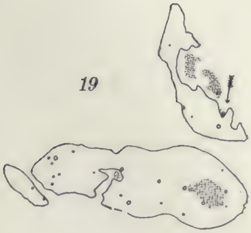

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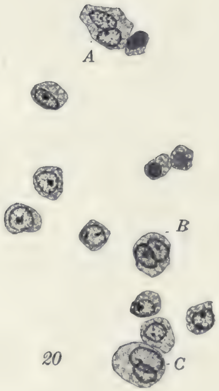


20

facing Pl. XLIX.

PLATE XLIX.

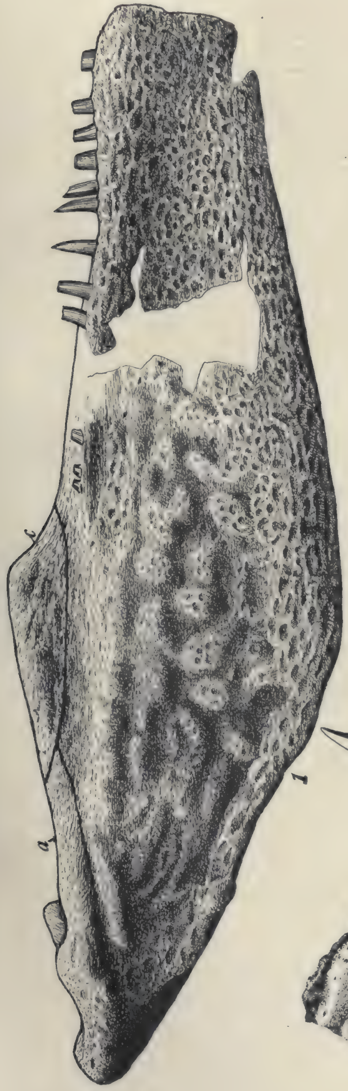
Fig. 1. External view of the right mandible of *Eryops willistoni.* × ½. Drawing by S. Prentice. *a* = articular; *c* = coronoid.

Fig. 2. Maxillary tooth of *Eryops willistoni.* × ½.

Fig. 3. Fragment of cranium, including portion of right orbit and showing very distinctly the suture bounding the anterior border of the right frontal. A portion of the supraorbital lateral line canal may be also detected. × ½. O = orbit.

Fig. 4. Cross section of mandibular tooth, showing pulp cavity and dental tubules. × 2.

Fig. 5. External view of anterior portion of the right mandible. × ½.



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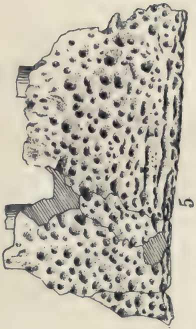

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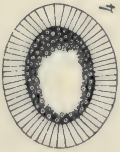

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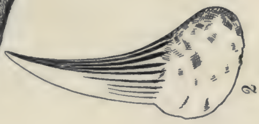

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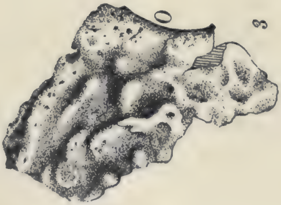
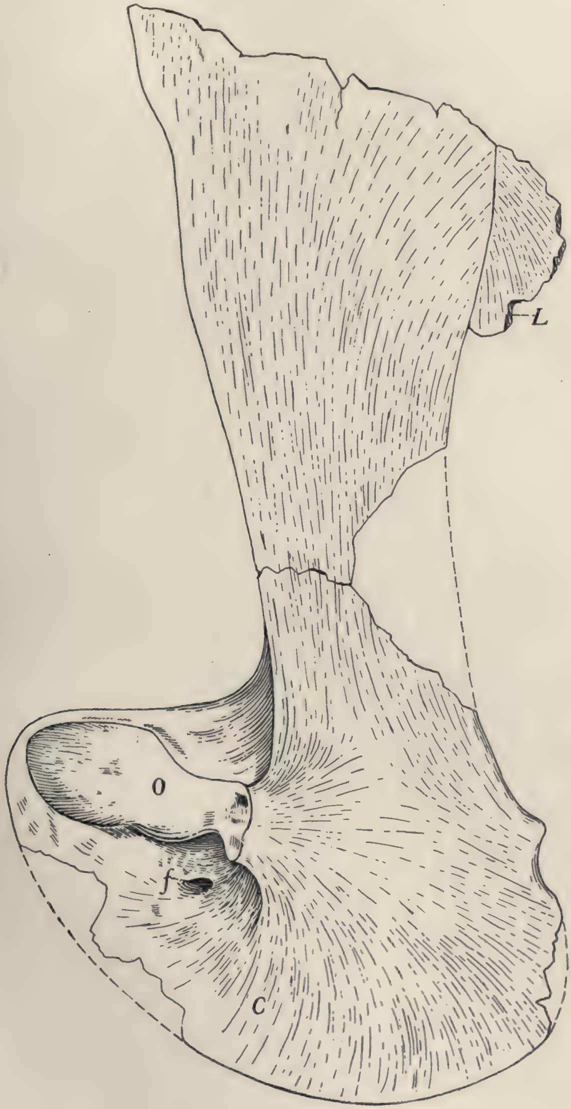


3

facing Pl. L.

PLATE L.

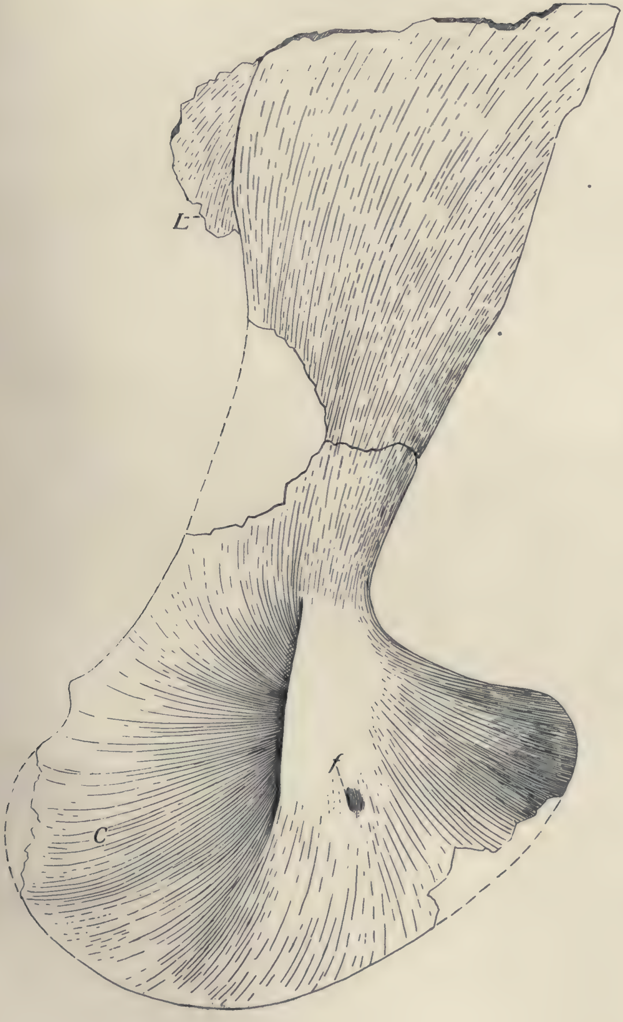
External view of the right coraco-scapula of *Eryops willistoni*. × ½.
C = coracoid portion of the coraco-scapula; *f* = foramen for artery;
L = cleithrum; *O* = humeral cotylus.


L
O
f
C

facing Pl. LI.

PLATE LI.

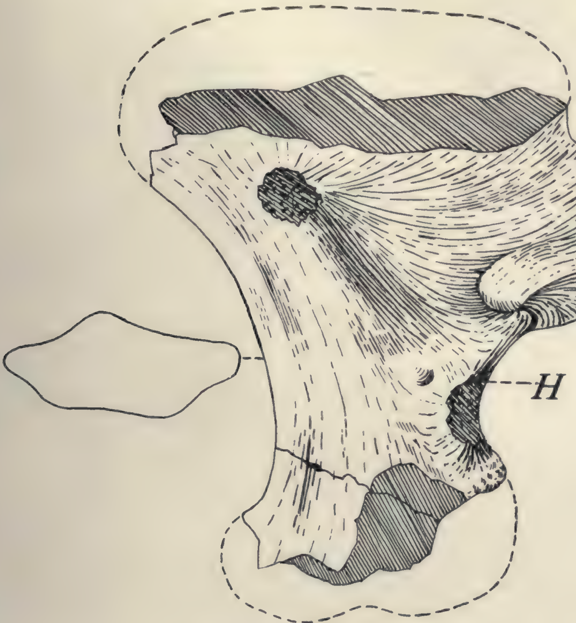
Internal view of coraco-scapula. *C* = coracoid portion; *f* = foramen; *L* = cleithrum. × ½.

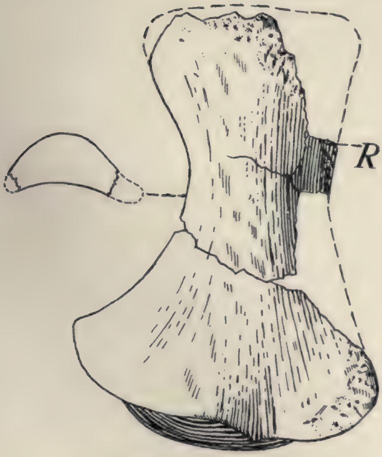

L
f
C

facing Pl LII

PLATE LII.

Arm bones of *Eryops willistoni.* × ⅔. *H* = humerus; *R* = radius; *U* = ulna. Cross sections of the various elements are shown at the sides.


H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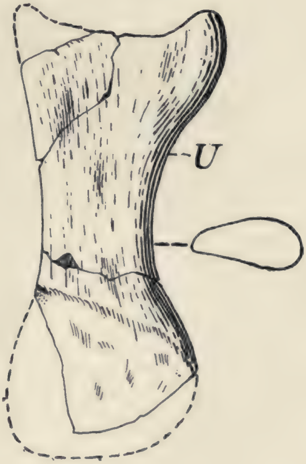

U

facing Pl LIII

PLATE LIII.

Fig. 1. Posterior view of right clavicle of *Eryops willistoni.* × ⅔.

Fig. 2. Ventral view of right clavicle. × ⅔.

Fig. 3. Ventral view of the posterior projection of the interclavicle of *Eryops willistoni.* × ⅔.

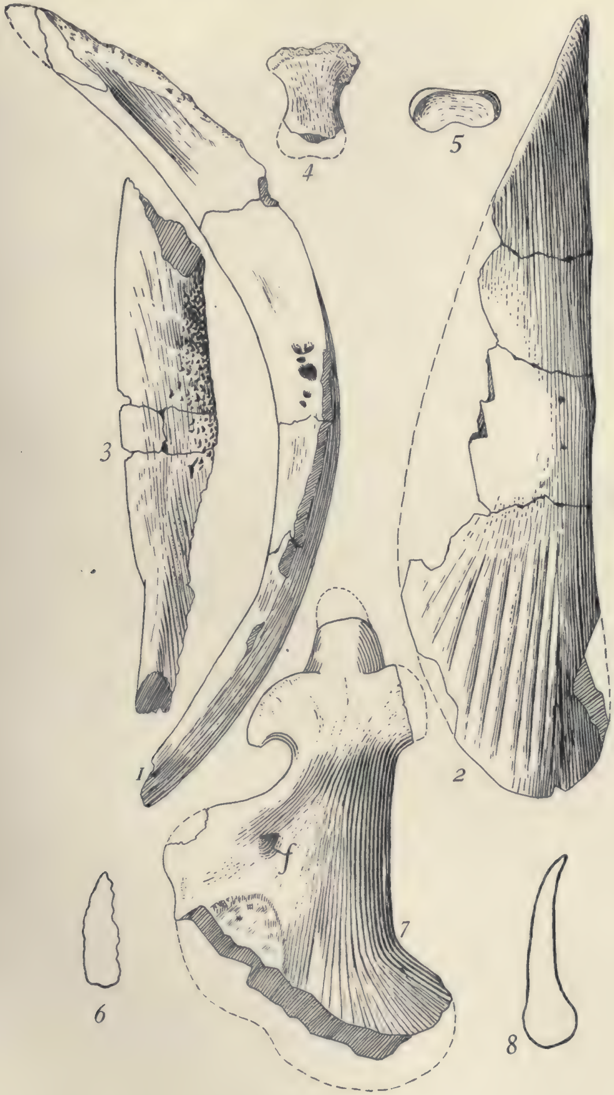
Fig. 4. Dorsal view of phalange (metacarpal ?). × ⅔.

Fig. 5. End view of same. × ⅔.

Fig. 6. Cross section of posterior projection of interclavicle.

Fig. 7. Anterior view of the right humerus. × ⅔. *f* = supracondylar arterial foramen.

Fig. 8. Cross section of the clavicle.


f

facing pl LIV

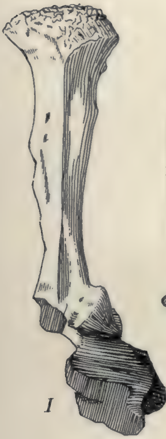
PLATE LIV.

FIG. 1. Posterior view of a dorsal vertebral spine, showing apical enlargement. × ⅔.

FIG. 2. Lateral view of three consecutive dorsal vertebræ. × ⅔.

FIG. 3. Ventral view of left sacral rib. × ⅔.

FIG. 4. Dorsal view of the same.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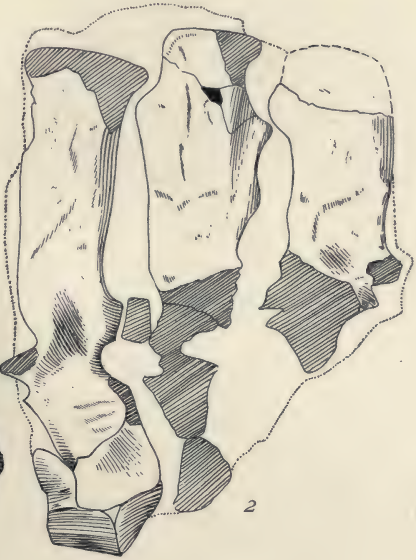
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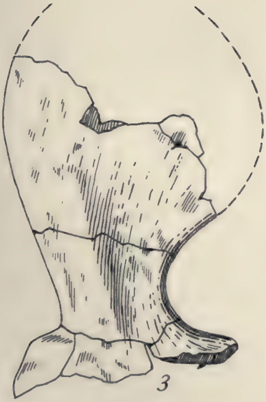
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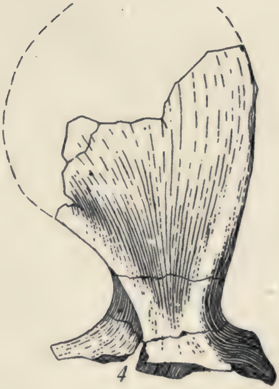
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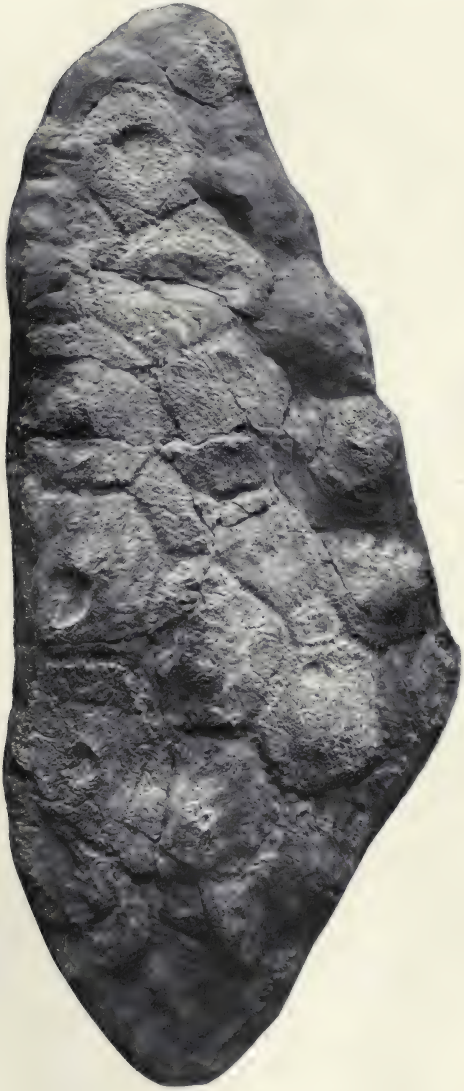
facing pl LV

PLATE LV.

The dorsal surface of the left ilium of *Stegopelta,* showing the dermal plates. × ¼.



facing pl. LVI

PLATE LVI.

FIG. 1. A large dermal spine which was possibly associated with the heavy bony girdles near the base of the tail. × ¼.

FIG. 2. One of the massive dermal plates of *Stegopelta,* which may have formed part of another girdle like the elements in figs. 6 and 7. × ½.

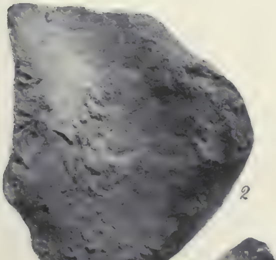
FIG. 3. The median dorsal scute between the ilia. × ¼.

FIGS. 4 and 5. The teeth of *Stegopelta.* × 1½.

FIGS. 6 and 7. Dorsal and posterior views of large bony girdle, which probably encircled the tail near the base. × ¼.

FIG. 8. Detail of the surface of the left ilium; one of the dermal scutes, one-half natural size.

FIG. 9. A heavy dermal plate, which may possibly have been associated with the element shown in figure 2 to form another girdle. (See Wieland, 1909, Amer. Jour. Sci., March, p. 251, fig. 6.) × ¼.



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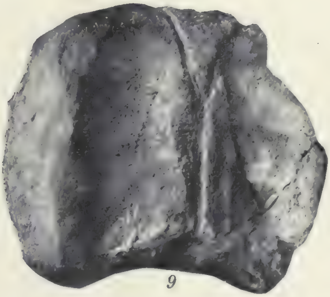

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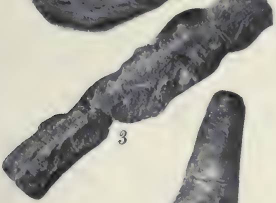

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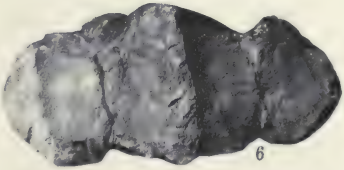

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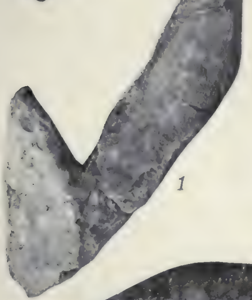

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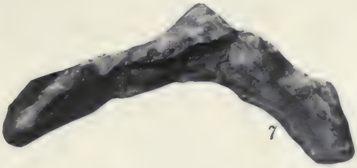

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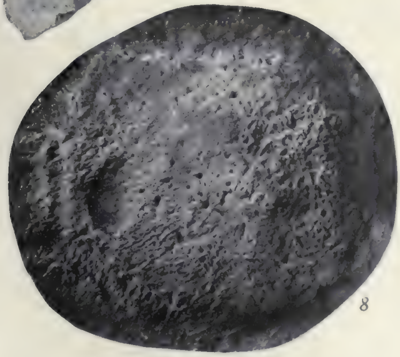

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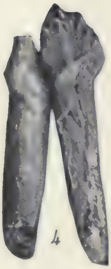

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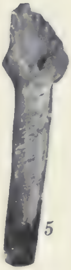
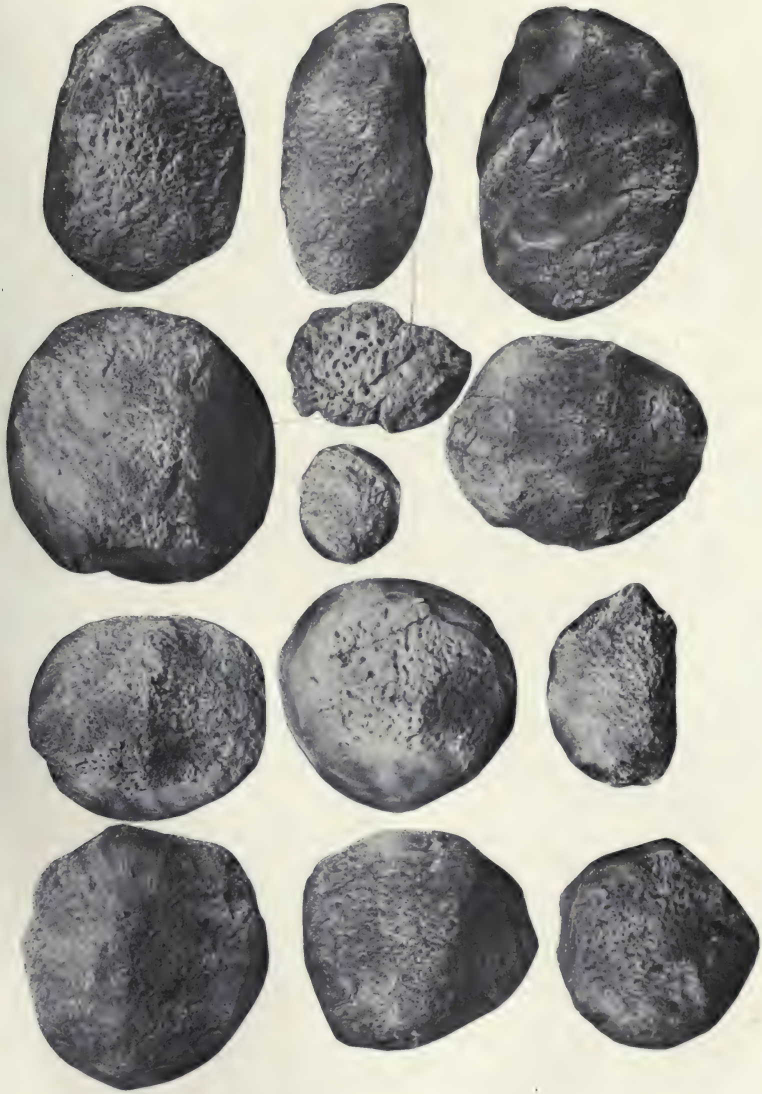


5

facing Pl. 57.

PLATE LVII.

Dorsal view of thirteen small dermal plates of *Stegopelta*, nearly natural size, showing the various shapes, sizes, and manner of ornamentation.



facing pl. 58

PLATE LVIII.

Fig. 1. The external surface of the right pubis. × ¼.

Fig. 2. The right pubis seen from the edge. × ¼.

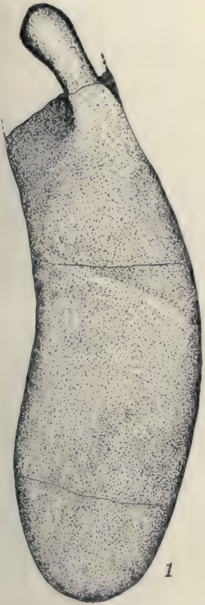
Fig. 3. The posterior view of an anterior caudal or a posterior sacral vertebra. × ¼.

Fig. 4. The lower portion of the right tibia, showing the firm union of the astragalus. One-half natural size.

Fig. 5. Lateral view of one of the dorsal vertebræ. One-half natural size.

Fig. 6. Posterior surface of a dorsal vertebra. × ½.

Fig. 7. A metatarsal of *Stegopelta* seen from above. × ½.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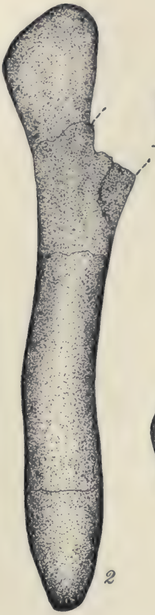
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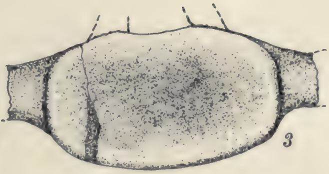
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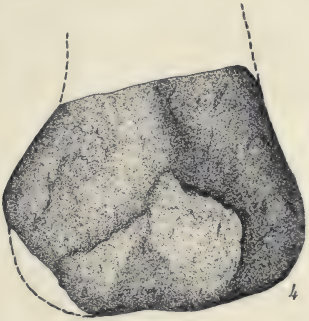
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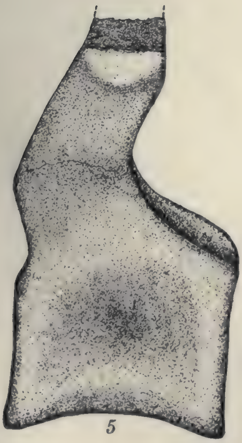
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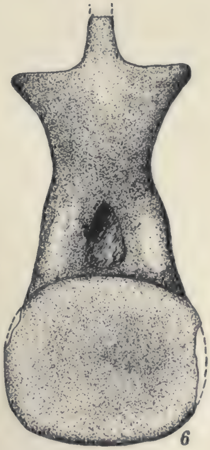
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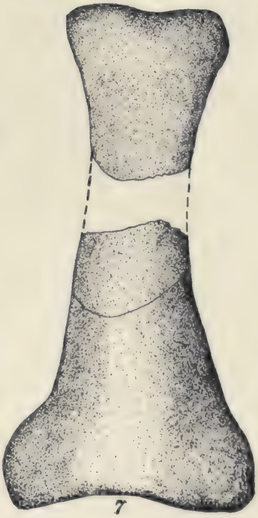
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facing p 159

PLATE LIX.

FIG. 1. Dorsal view of an anterior caudal vertebra. × ¼.

FIG. 2. A cross section of the sacrum to show the sacral enlargement. × ½.

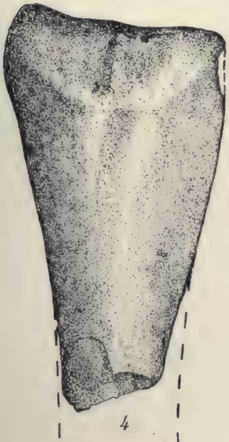
FIG. 3. A small dermal spine. × ½.

FIGS. 4 and 5. Upper and lower portions of right fibula. × ¼.

FIGS. 6 and 7. Dorsal surface of posterior and anterior segments of the sacrum.

FIG. 8. The left ulna seen from behind. One-tenth natural size.

FIG. 9. The left ulna seen from the side. One-tenth natural size.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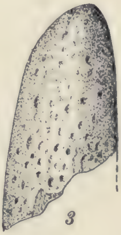
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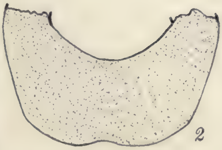
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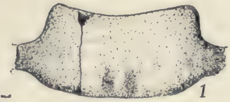
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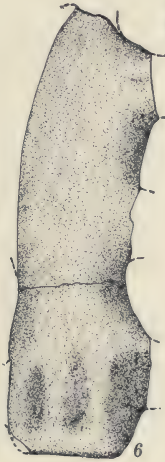
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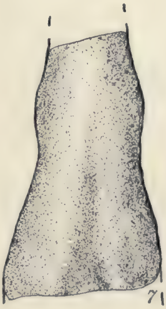
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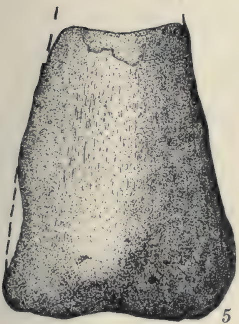
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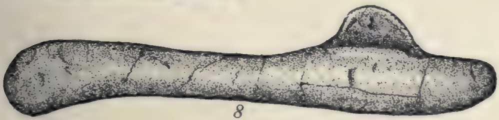
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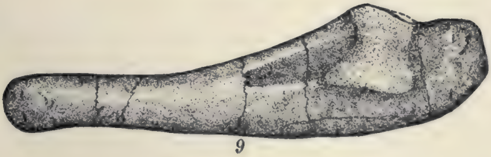
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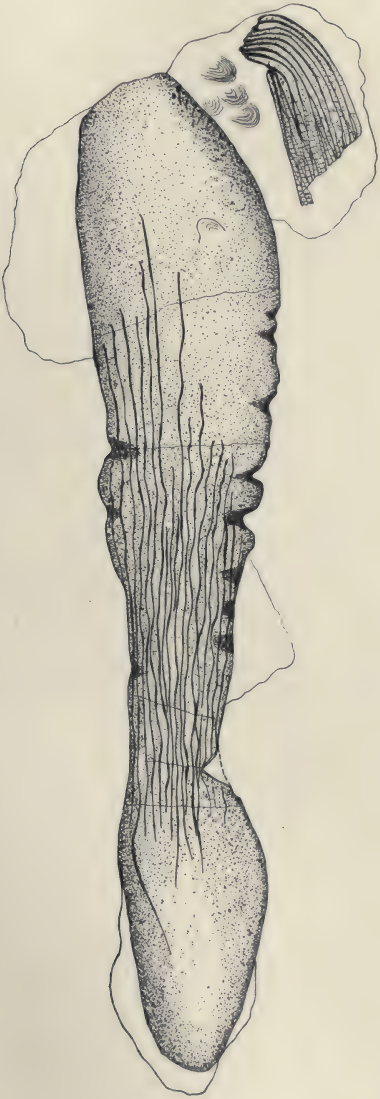
facing pl 60

PLATE LX.

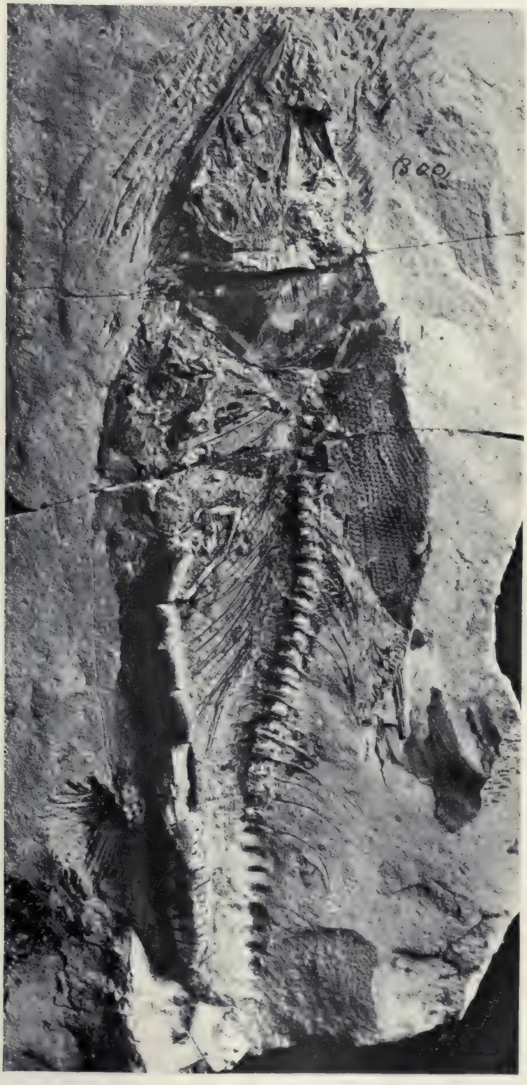
The stomach of *Empo nepaholica* Cope from the Niobrara Cretaceous. The longitudinal muscular plicæ are indicated by heavy lines. × ½.



facing pl. 61.

PLATE LXI.

The specimen of *Thrissopater intestinalis* Moodie. × ⅔.


B601

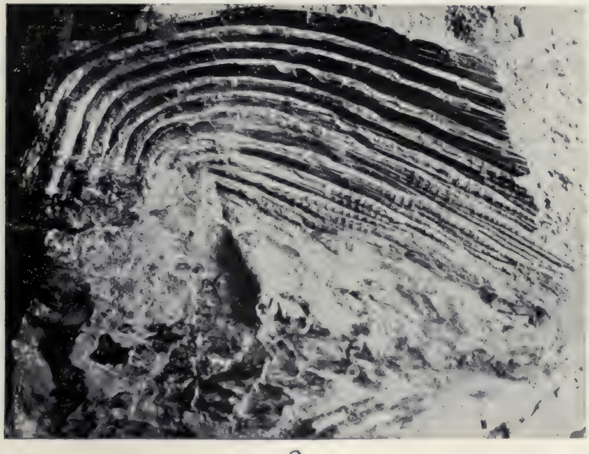
facing pl 62

PLATE LXII.

FIG. 1. Photograph of the alimentary canal of the Buffalo fish, *Ictiobus bubalus* Raf., from the Kaw river, showing the similarity in the form of the intestines to that preserved in the fossil *Thrissopater intestinalis* Moodie. × ½.

FIG. 2. Photograph of the right pectoral fin of *Empo nepaholica* Cope. × ¾.

1



2

facing pl. 63

PLATE LXIII.

Upper figure: Lateral view of female of *Prorocorypha snowi,* new gen. and sp. × 2.

Second figure: Lateral view of male of *Prorocorypha snowi.* × 2.

Left of three middle figures: Lateral view of apex of male abdomen of *Prorocorypha snowi.* × 4. (The supra-anal plate of the specimen from which the artist made the drawing is broken. It is long, as in the female.)

Middle of three middle figures: Dorsal view of head and pronotum of female of *Prorocorypha snowi.* × 2.

Right of three middle figures: Lateral view of apex of female abdomen of *Prorocorypha snowi.* × 4.

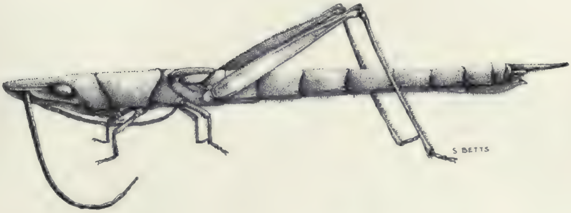
Next to bottom row, left figure: Dorsal view of head and pronotum of *Scirtetica ritensis,* new species. × 2.

Next to bottom row, right figure: Lateral view of type specimen of *Scirtetica ritensis.* × 2.

Bottom row, left figure: Wing of *Scirtetica ritensis.* × 2.

Bottom row, middle figure: Lateral view of apex of female abdomen of *Scirtetica ritensis.* × 2.

Bottom row, right figure: Lateral view of male abdomen of *Scirtetica ritensis.* × 2. (This figure was drawn by the artist from a specimen not studied by the author.)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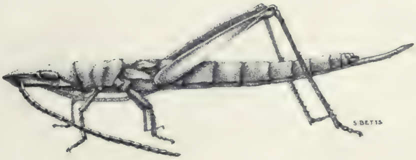
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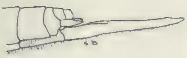
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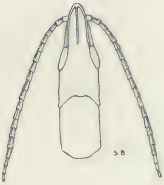
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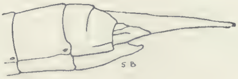
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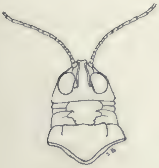
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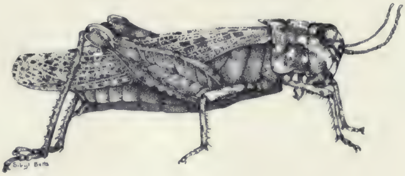
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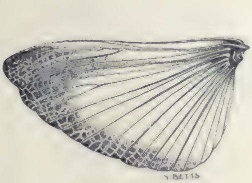
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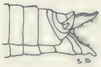
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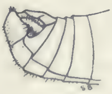
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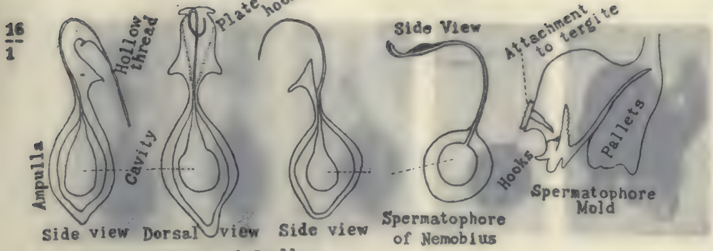
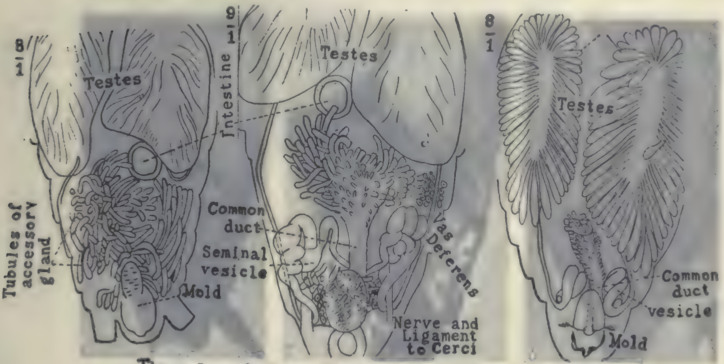

16
1
Hollow thread
Plate with hooks
Ampulla
Cavity
Side View
Attachment to tergite
Hooks
Pallets
Spermatophore Mold

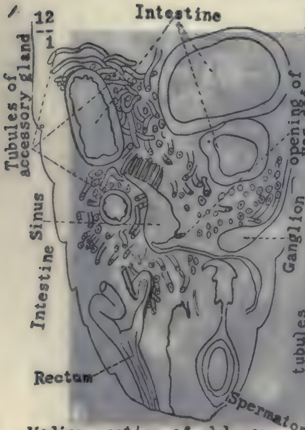
Side view Dorsal view Side view

Spermatophores of Gryllus

Spermatophore of Nemobius


8
1
Testes
Tubules of accessory gland
Mold
9
1
Intestine
Testes
Common duct
Seminal vesicle
Vas Deferens
Nerve and Ligament to Cerci
8
1
Testes
Common duct
vesicle
Mold

Three Dorsal Dissections of the Abdomen of Gryllus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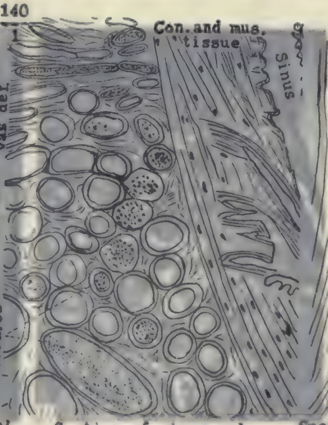
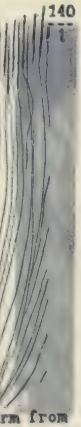
1
Intestine
Tubules of accessory gland
Sinus
Intestine
opening of vas def
Ganglion
Rectum
Spermatophore

Median section of abdomen

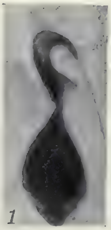

140
1
Con.and mus. tissue
Sinus
tubules

Section of sinus and secreting tubules



Sperm from spermatophore

facing p. 24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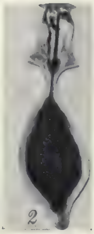
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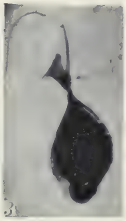
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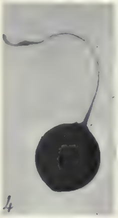
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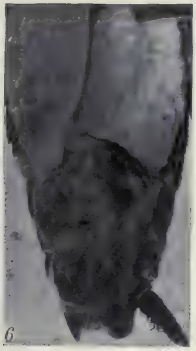
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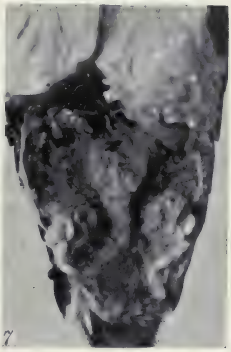
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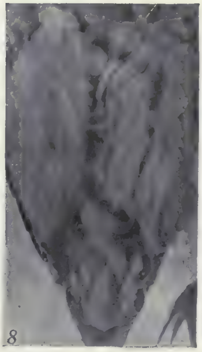
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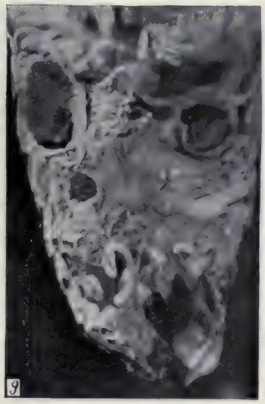
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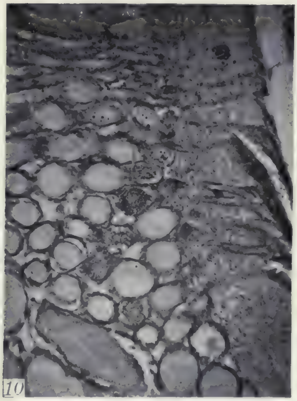

10

11

PLATE LXV.

FIGS. 1 to 10, inclusive.—Polar views of the equatorial plate from spermatogonial cells, each showing the entire number of chromosomes. In figs. 1, 2 and 4 the possible pairing of equal elements is shown. There are ten pairs. Nos. 1-1 are the largest two spermatogonial chromosomes, which form the largest chromosome of the spermatocyte group. No. 11 is unpaired, and is the accessory chromosome. In figs. 5 to 10, inclusive, the connecting bands of linin are not shown.

FIG. 11.—Lateral view of the spindle in metaphase from a young spermatogonial cyst.

FIG. 12.—Same from an older spermatogonial cyst.

FIG. 13.—Beginning anaphase from an older spermatogonial cyst, showing the usual confluent condition of the chromatin.

FIG. 14.—Late spermatogonial anaphase.

FIG. 15.—A section of an entire spermatogonial cyst, showing the cells in different stages of division. The polarity shown is typical.

FIG. 16.—Early spermatogonial telophase.

FIG. 17.—Polar view of the same, in which all twenty-one members of the complex can be distinguished. (*x*) Accessory chromosome.

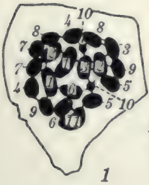
FIG. 18.—Late telophase, from a young spermatogonial cyst.

FIGS. 19 and 20.—Nuclei of spermatogonial cells, showing the chromatin at the point of greatest diffusion. The reticular structure is still evident.

FIG. 21.—A typical spermatogonial nucleus, showing the beginnings of the reorganization of the nuclear chromatin.

FIGS. 22 to 28, inclusive.—Successive stages in the re-formation of the spermatogonial chromosomes.

FIGS. 29 to 33, inclusive.—Nuclei in the process of synizesis. (*x*) Accessory chromosome. (*t*) Nuclear membrane. (*c*) Chromatin mass.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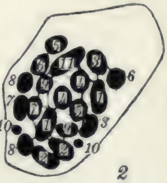
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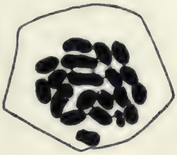
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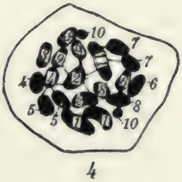
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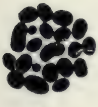
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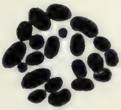
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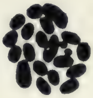
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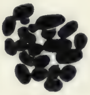
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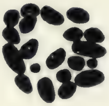
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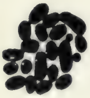
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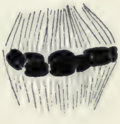
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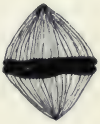
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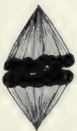
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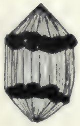
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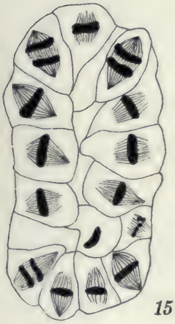
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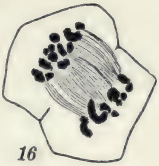
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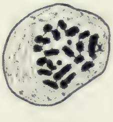
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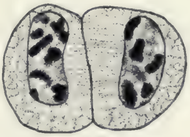
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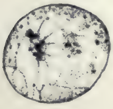
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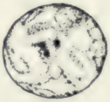
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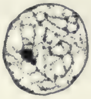
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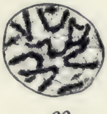
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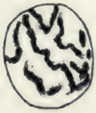
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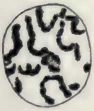
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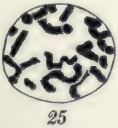
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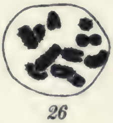
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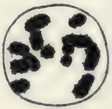
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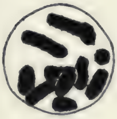
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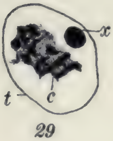

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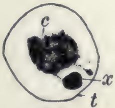

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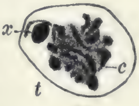

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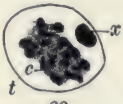

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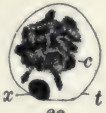

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PLATE LXVI.

FIG. 1.—An early stage of the spermatocyte nucleus, succeeding synizesis. (x) Accessory chromosome. (p) Plasmasome.

FIGS. 2 and 3.—Same as fig. 1.

FIG. 4.—Slightly later stage of the spermatocyte nucleus than is shown in figs. 1, 2 and 3. The chromatin is more diffuse and the accessory chromosome (x) is elongated, granular, and stains more deeply than the other chromatin.

FIG. 5.—A spermatocyte nucleus at the period of greatest diffusion. The chromatin is reticular. (p) Plasmasome. (x) Accessory chromosome more condensed than the form shown in fig. 4.

FIG. 6.—Same as fig. 5. The accessory is a homogeneous chromatin rod and the plasmasome reaches its maximum size in this stage.

FIG. 7.—Spermatocyte nucleus in early prophase, showing the first signs of chromosome reorganization. (p) Vacuolated plasmasome. (x) Accessory chromosome. The difference in the consistency of these two bodies is apparent in iron-hæmatoxylin preparations which were stained for a shorter time, comparatively, or which were subjected to a longer extraction process.

FIG. 8.—Spermatocyte nucleus, showing the beginnings of tetrad formation and the accompanying phenomenon, the decrease in size of the plasmasome.

FIG. 9.—Later spermatocyte prophase. The plasmasome becomes spherical as it disappears.

FIGS. 10 and 11.—Two parts of the same nucleus drawn from adjacent sections. There are thirteen bodies, all of which are shown. The plasmasome has diminished greatly in size. (m) The univalent halves of the small chromosome.

FIGS. 12 and 13.—Spermatocyte cells in early prophase. The nuclear wall in fig. 12 is not shown. The plasmasome is very lightly stained, in marked contrast to the accessory, which holds the stain much longer.

FIG. 14.—Accessory chromosomes drawn from spermatogonial cells in metaphase. For the method of identification see text.

FIG. 15.—Accessory chromosomes from cells of the same stage and preparation as that of fig. 12, where there is no trouble in identifying this element.

FIG. 16.—Tetrads from the same stage and preparations as figs. 12 and 13. (a) Largest form. (b) and (c) Typical forms of the cross. (d) The small chromosome, the halves of which are not usually so close together at this time.

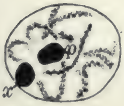
FIG. 17.—Portion of a spermatocyte nucleus in late prophase, showing the diminishing plasmasome (p) and the halves of the small chromosome (m).

FIGS. 18 and 19.—Portions of the same spermatocyte nucleus appearing in adjacent sections, showing thirteen elements—nine tetrads, two m-chromosome diads, the accessory chromosome, and the plasmasome. The plasmasome has almost entirely disappeared.

FIGS. 20 and 21.—Same as figs. 18 and 19.

FIGS. 22 and 23.—Same as the two previous figures.

FIGS. 24 and 25.—Same as above. The nuclear wall in fig. 25 is not shown.



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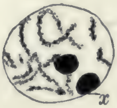

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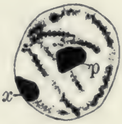

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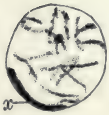

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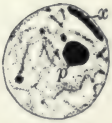

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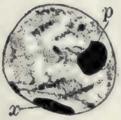

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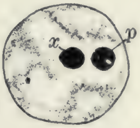

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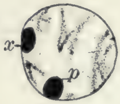

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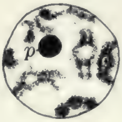

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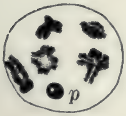

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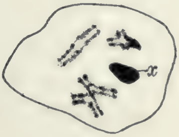

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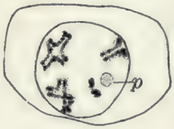

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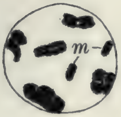

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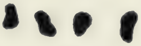

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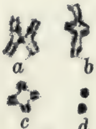

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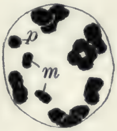

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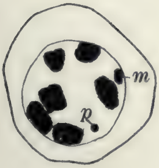

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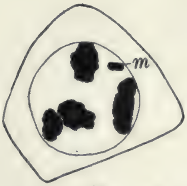

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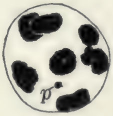

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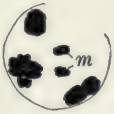

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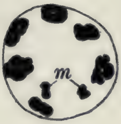

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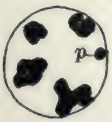

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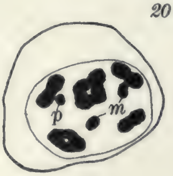

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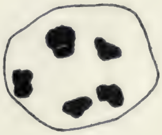

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facing pl. 67

PLATE LXVII.

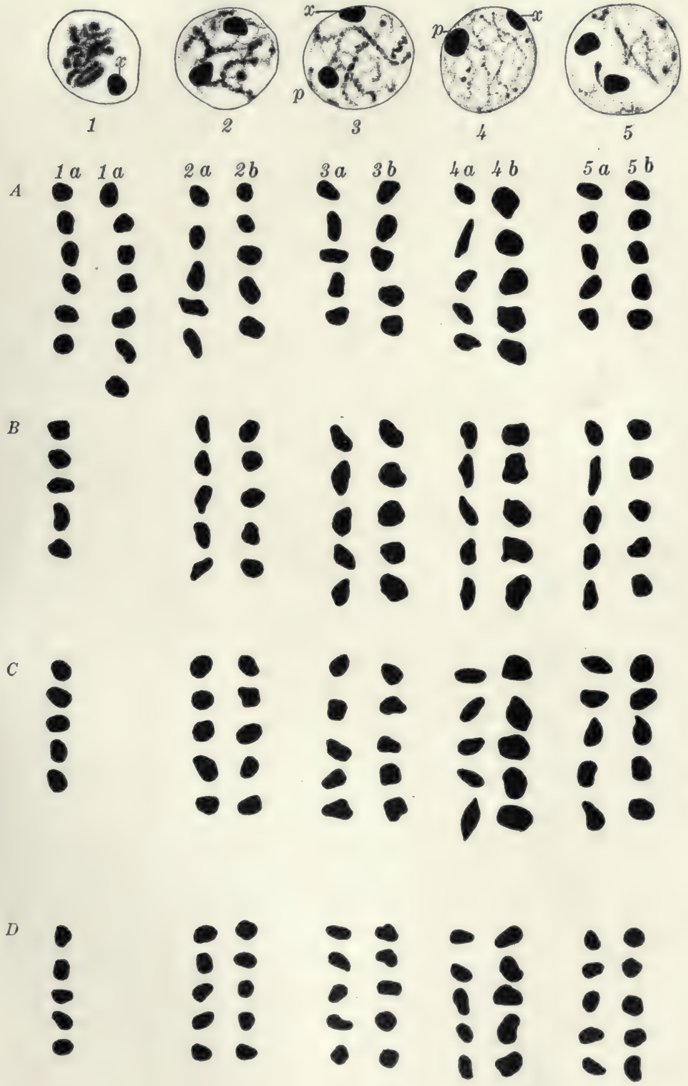
FIG. 1.—Nucleus in the process of synizesis. (*x*) Accessory chromosome. 1*a*.—Drawings of accessory chromosomes from nuclei similar to fig 1. *A*, *B*, *C* and *D* indicate the four individuals from which these comparative drawings were made.

FIG. 2.—Spermatocyte nucleus, immediately after synizesis, showing both accessory chromosomes and the plasmasome. 2*a*.—Accessory chromosomes from the same stage as is shown in fig. 2. 2*b*.—Plasmasomes from the same nuclei as the accessory chromosomes in 2*a*. The opposite elements in columns 2*a* and 2*b* are from the same nucleus. The same holds true for columns 3*a* and 3*b*, 4*a* and 4*b*, 5*a* and 5*b*.

FIG. 3.—Spermatocyte nucleus, showing a later stage than fig. 2. 3*a*.—Accessory chromosomes from the same stage as fig. 3. 3*b*.—Plasmasomes from the same stage as fig. 3. See explanation of fig. 2, same plate.

FIG. 4.—Spermatocyte nucleus at the period of maximum diffusion and largest plasmasome growth, deeply stained. 4*a*.—Accessory chromosomes from same state as fig. 4. 4*b*.—Plasmasomes from same stage as fig. 4. See explanation of fig. 2, same plate.

FIG. 5.—Spermatocyte nucleus, showing the beginning of chromosome reorganization. 5*a*.—Accessory chromosomes from the same stage as fig. 5. 5*b*.—Plasmasomes from the same stage as fig. 5. See explanation of fig. 2, same plate.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2
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4
5
1a
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2b
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3b
4a
4b
5a
5b
A
B
C
D

facing pl 68

PLATE LXVIII.

FIGS. 1 to 10, inclusive.—The chromosome complex of the first spermatocyte in metaphase. (*x*) Accessory chromosome.

FIG. 5.—An unusual condition of the first spermatocyte metaphase, showing twelve elements. *a-a*.—Probably the disjoined halves of one of the larger chromosomes which normally occurs in the ring.

FIG. 11.—Drawings of the accessory chromosome from cells of the cyst from which fig. 6 was made, showing the constancy in size in this element within a single cyst.

FIG. 12.—Drawings of the accessory chromosome from cells of the cyst from which fig. 7 was made.

FIG. 13.—Drawings of the accessory chromosome from cells of the cyst from which fig. 8 was made.

FIG. 14.—Drawings of the accessory chromosome from cells of the cyst from which fig. 9 was made.

FIG. 15.—Drawings of the accessory chromosome from cells of the cyst from which fig. 10 was made.

FIG. 16.—Lateral view of first spermatocyte in beginning anaphase. (*x*) Accessory chromosome. The cell membrane is shown.

FIG. 17.—First spermatocyte spindle, in longitudinal section through the accessory chromosome (*x*). (*a*) and (*b*) Chromosomes of the ring at equal distances from (*m*), the central small chromosome. The accessory chromosome lies outside of the ring, causing the asymmetry of the spindle, as drawn.

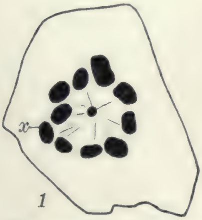
FIG. 18.—Same view of a slightly later stage, showing the typical irregularity in the movements of the accessory chromosome (*x*) and the central small chromosome (*m*) with respect to those of the ring (*a*) and (*b*).

FIG. 19.—Later anaphase, showing the difference in organization between the accessory chromosome (*x*) and the ordinary chromosomes.

FIGS. 20, 21 and 22.—Later successive stages of the first spermatocyte anaphase. (*x*) Accessory chromosome.

FIGS. 23, 25 and 26.—First spermatocyte telophases, in which the accessory chromosome (*x*) may still plainly be identified.

FIG. 24.—Telophase of first spermatocyte. (*x*) Unusual element, which is probably an undivided accessory chromosome or a persistent plasmasome.



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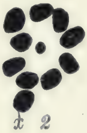

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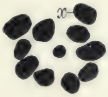

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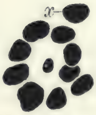

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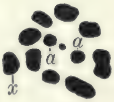

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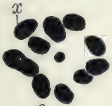

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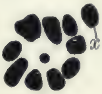

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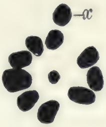

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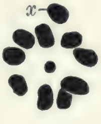

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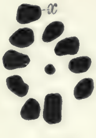

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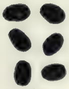

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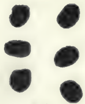

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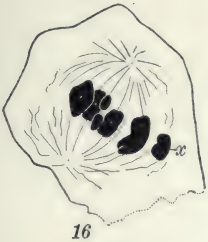

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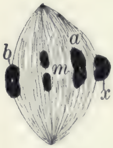

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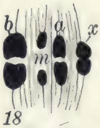

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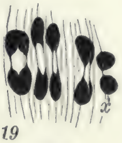

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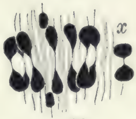

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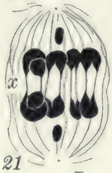

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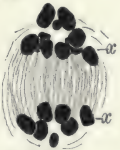

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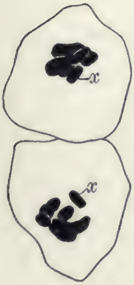

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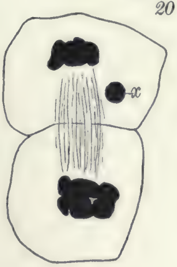

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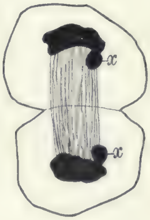

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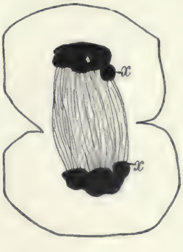

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PLATE LXIX.

FIGS. 1, 2 and 3.—Polar views of the single daughter groups of chromosomes resulting from the first spermatocyte division. This stage is of very brief duration following immediately that in figure 25, plate LXVIII.

FIG. 4.—A group of drawings of the accessory chromosome from stages such as are shown in figures 1, 2 and 3.

FIGS. 5, 6, 7 and 8.—Polar views of the second spermatocyte complex. Note difference in arrangement of the chromosomes compared with those of first spermatocytes.

FIG. 9.—Oblique view of a late first spermatocyte telophase. One whole daughter group is shown and part of the other.

FIGS. 10, 11 and 12.—Lateral view of second spermatocyte spindle in metaphase. (x) Accessory chromosome. (m) Small central chromosome.

FIG. 13.—Lateral view of early anaphase, second spermatocyte.

FIG. 14.—Later stage of the same. (x) Accessory chromosome.

FIG. 15.—Same as figures 13 and 14, showing all of the chromosomes. (x) Accessory chromosome.

FIG. 16.—Same as figure 14.

FIG. 17.—Slightly later stage, showing the beginnings of the formation of a dividing cell membrane. Note that the daughter groups of chromosomes are entirely coalesced. This is typical of these later stages.

FIG. 18.—Same as figure 14.

FIG. 19.—Group of accessory chromosomes drawn from cells such as are shown in figure 18, showing the constancy in size of the lagging element (x).

FIGS. 20, 21, 22, 23, 24 and 25.—Later stages in the second spermatocyte division, showing the behavior of the accessory chromosome (x). Note the dividing cell wall and persistent spindle fibers which identify beyond a doubt the two cells shown in each figure as daughter cells of the same first spermatocyte.

FIGS. 26 and 28.—Later stage of the same after the formation of the nuclear membranes. (x) Accessory chromosome.

FIG. 27.—Later stage of the same in which the spindle fibers are fading.

FIG. 29.—Still later stage in which the two chromatin masses are breaking up and the ordinary chromatin appears granular. (x) Accessory chromosome.

FIG. 30.—A group of drawings, showing the typical appearance of the daughter nuclei of the second spermatocyte which have received the accessory chromosome in the second maturation division.

FIG. 31.—A group of drawings showing the early development of the spermatid which received the accessory chromosome in the second maturation division.

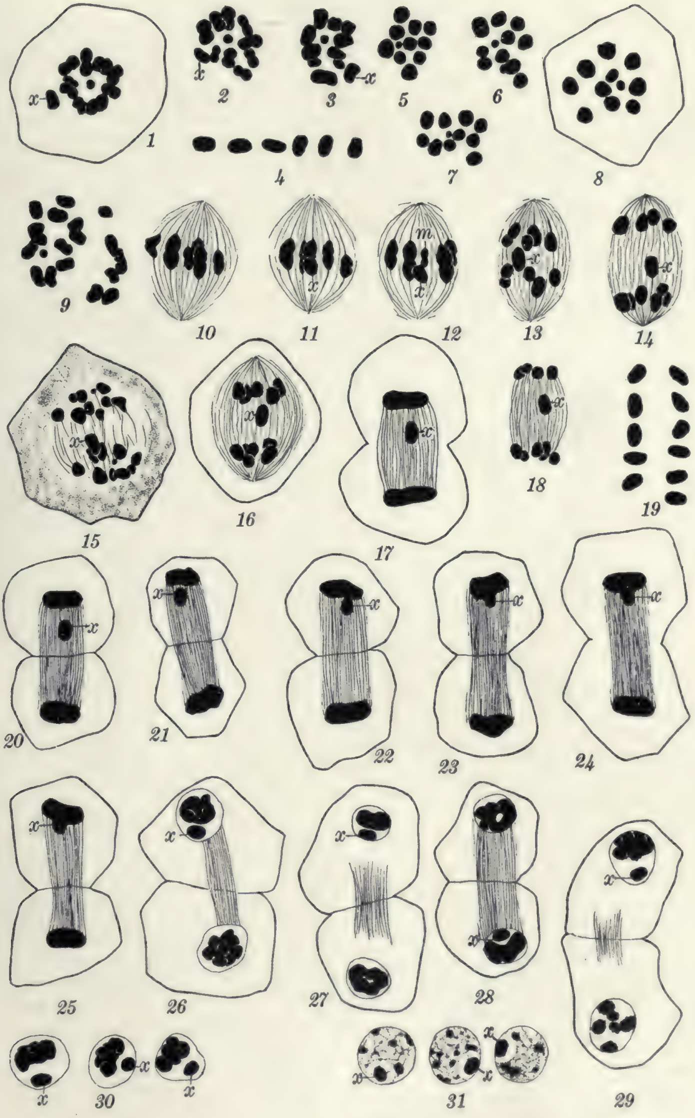
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PLATE LXX.

These photomicrographs were made with a Zeiss 2mm., 1.40 N. A. apochromatic objective and No. 4 projection ocular, the camera bellows being extended so as to place the sensitive plate at a distance of thirty-one inches above the object. Illumination was furnished by Welsbach mantle, the light passing through a Watson Parachromatic oil immersion condenser with the diaphragm set at N. A. 1.0. The original magnification is 1500 diameters which, in reproduction, has been reduced to 1000 diameters. Considerable detail has been lost in reproduction, especially in figures 3, 7 and 8.

FIG. 1.—Polar view of spermatogonial metaphase, showing 21 chromosomes.

FIG. 2.—Same as figure 1.

FIG. 3.—Same as figure 1.

FIG. 4.—First spermatocyte prophase, in which the accessory chromosome is bent in the middle. This is the nearest approach to the spireme condition found in *Anasa.*

FIG. 5.—Later prophase with the accessory extended and showing the longitudinal split.

FIG. 6.—Same stage as in figure 5.

FIG. 7.—A portion of three cysts appears in this photograph. In the lower one the last generations of spermatogonial chromosomes are seen in several cells. At the upper right-hand corner are four cells in synizesis.

FIG. 8.—Parts of three cysts are included in this picture. The cells in each are in some stage of synizesis. The presence of the accessory chromosome on the periphery of the nucleus and of the plasmasome in the synizetic knot is demonstrated in several cells. The stages shown in figures 7 and 8 precede the ones represented in figures 4, 5 and 6.

FIG. 9.—Post-synizetic stage, in which the peripheral accessory and the more central plasmasome are shown in several cells. This may be compared with a similar condition in cells prepared according to the method of Foot and Strobell, as shown in their figures 11 and 12, in order to judge of the correctness of their belief that the smear method preserves delicate detail better than sections. It may be pointed out also that there is little liability to confuse either of the nucleolar bodies with karyosomes resulting from concentrations of the chromatin elsewhere. Wilson's slide 949*b*. Photos 1 to 9 from sections.

FIG. 10.—Chromosomes of the first spermatocyte metaphase, smear preparation. The lowermost chromosome is the accessory. It is seen to have one plane of division, while the others have more or less distinct second planes indicated. In this cell the five lower chromosomes have dried thinner and spread more than the upper six and show wrinkles and other distortions. Wilson's Woods Hole "x" slide.

FIGS. 11-15.—Photographs from sections on Wilson's slide 949*b*, showing the accessory chromosome and plasmasome in the first spermatocyte prophase at about the same stage as that of figure 9. It is difficult to

facing pl. 70

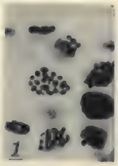
get several nuclei close together with the two elements in focus at the same time, but most of these show at least two cells. Figure 11 is in focus at the level of the upper part of the nucleus and shows the accessory extended as in figures 5 and 6.

FIGS. 16-20.—Photographs from smears on Lefevre's slide 30, showing the late prohases of the first spermatocyte. The accessory is distinguished, as Foot and Strobell point out, by having two halves lying side by side without lateral extensions. There is no indication of a second plane of division, as may easily be seen in figures 16 and 20. In figure 20 there appear thirteen elements.

FIGS. 21-26. These are from smears, and show the chromosomes of the first spermatocyte in metaphase. The great difference in the size of the chromosomes, due to the variation in the extent of spreading, upon drying may be judged by comparing figure 22 with figures 23 and 10. In figure 23 there are twelve elements, one much lighter than the others, which may be interpreted as an unsually resistant plasmasome which has persisted much longer than common. In all of these the accessory may be identified both by its position and by the single plane of cleavage indicated. It has been injured in the cell represented in figure 23, where it is seen next to the plasmasome with one corner cut sharply off.

FIGS. 27 and 28.—Photographs of the first spermatocyte metaphase, polar view, showing the typical arrangement of the chromosomes. The accessory lies without the ring and the *m*-chromosome in the center. These prints are from the *same negative* and show how it is possible to vary the apparent size of structures even by printing. Wilson's section.

FIGS. 29-33.—Polar views of first spermatocyte metaphases from sections. In order to get several cells to show together the focus was shifted during exposure in making photograph 31 so that the outlines are not sharp. In figure 29 the accessory does not show, being just out of focus in the lower cell. From these illustrations it may be seen that while there is a general agreement in the arrangement of the chromosomes in the equatorial plate, it may be modified in details. Wilson's sections.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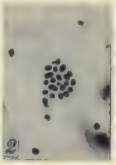
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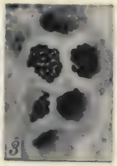
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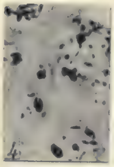
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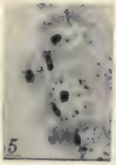
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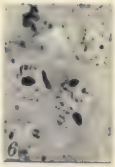
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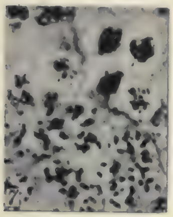
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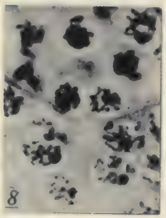
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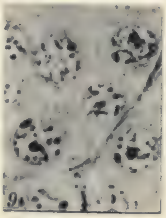
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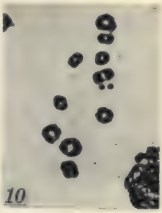
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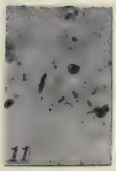
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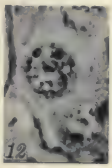
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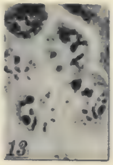
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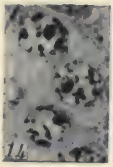
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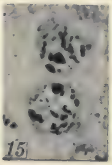
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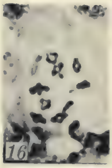
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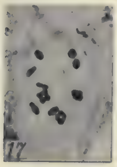
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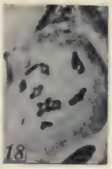
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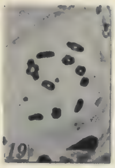
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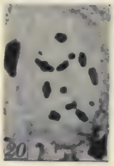
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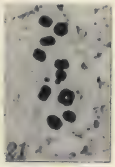
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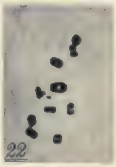
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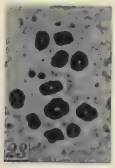
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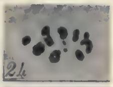
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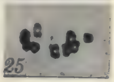
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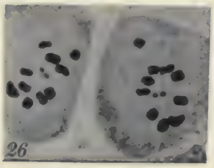
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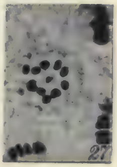
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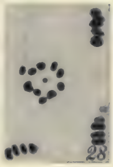
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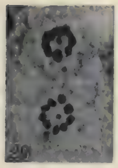
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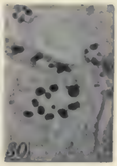
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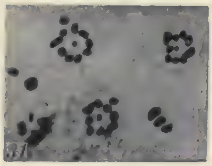
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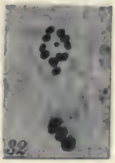
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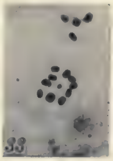
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McCLUNG, PHOTO

COCKAYNE-BOSTON

PLATE LXXI.

FIG. 1.—Lateral view of two second spermatocytes in early anaphase. It is apparent in both of these that the accessory chromosome is already in movement to one of the poles, in the upper cell to the right and in the lower to the left. The accessory in the upper cell already has its longer axis parallel to that of the spindle. Smear by Wilson.

FIG. 2.—Lateral view of first spermatocyte in metaphase or early anaphase. The accessory is the lowermost chromosome. All the elements are clearly seen to be divided. This is a slightly earlier stage than the ones of the second spermatocytes in figure 1 and should be compared with them in order to see the difference in the behavior of the accessory in the two divisions. Smear by Lefevre.

FIG. 3.—Mid-anaphase of the first spermatocyte, showing the full complex of chromosomes in each daughter cell. The accessory is the lowermost one in each group and is slightly removed from the others. Smear by Wilson.

FIG. 4.—Late anaphase of the first spermatocyte mitosis. The accessory lies to the right of each daughter group at the same level. Smear by Lefevre.

FIG. 5.—Mid-anaphase of the first spermatocyte, oblique view. The accessory to the right of each daughter group.

FIG. 6.—Mid-anaphase of the first spermatocyte anaphase, lateral view. The accessory at the lower end of each daughter group.

FIG. 7.—Very late anaphase of the first spermatocyte division, lateral view, with the accessory chromosome of each group proximal to the equatorial plate. Smear by Wilson.

FIG. 8.—Late anaphase of the first spermatocyte mitosis, showing the divided accessory accompanying each daughter group of chromosomes. Smear by Lefevre.

FIG. 9.—Like figure 8. Smear by Lefevre.

FIG. 10. Similar to figures 8 and 9. Smear by Lefevre. This series of anaphases of the first spermatocyte indicate, I think, that the accessory is characterized by an independence of movement and position in the group of chromosomes rather than by a "lagging" tendency. It does not in any case, apparently, anticipate the poleward movement of the other chromosomes, but takes part in the general division. On account of its peripheral position and slighter relation to the plate of chromosomes it is crowded back and therefore lies below the daughter mass of chromatin. Its position in the metaphase of the second spermatocyte depends upon the degree to which it is crowded aside in the telophase of the first. If it maintains its peripheral position at the level of the other chromosomes it is then an eccentric element in the metaphase of the second spermatocyte. If, however, it lies beneath the other chromosomes in the telophase it may become included within the ring of chromosomes in the next metaphase.

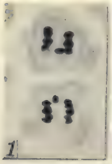
FIG. 11.—Polar view of second spermatocyte metaphase. In the lower cell three chromosomes are shown in lateral view. The difference in the arrangement of the chromosomes, as compared with the first spermatocyte, is striking and apparent. Section by Wilson.

facing pl. 71.

FIG. 12.—Similar to figure 11. Compared with the cell shown in the preceding figure it is seen that the arrangement of the chromosomes is different and that both are unlike that of the first spermatocyte where the *m*-chromosome practically always lies within a ring of larger chromosomes. The upper cell in figure 11 shows how close the resemblance to the first spermatocyte may be, on the contrary. Section by Wilson.

FIGS. 13-27.—Photomicrographs of smears, mostly from slides by Wilson, showing the behavior of the accessory in the second spermatocyte. It will appear from these, I think, that while the accessory may lie near the equatorial plate in the early and mid anaphases, when actual division of the cell has occurred the position of the accessory in only one of the two daughter cells may be determined. Of particular importance in this connection is figure 15 where numerous cells in telophase are in focus at one time. Each one of these demonstrates beyond question the unilateral movement of the accessory. This area is but a small part of a much larger one on the slide, where more than a hundred similar cells show, without exception, the same undivided condition of the unpaired element. The lagging chromosome is recognized by all to be the accessory. It is seen here in all the divided cells to pass without division into but one of the two daughter derivatives. In comparing these figures with those of Foot and Strobell it should be borne in mind that these cells are without question completely divided, that numbers of them are shown together, and that the whole cell body is represented, so that there can be no question of the relation between the members of the pairs of chromosome groups. Their figures, on the contrary, are of single cells, mostly in early or mid anaphases, in which the cell body does not appear. The consistent behavior of the accessory chromosome in the different cell generations is worthy of attention also. Wherever it is found it tends to isolate itself somewhat from the rest of the chromosomes and to behave with some independence. The argument of Foot and Strobell is based on conformity to one type on the part of the accessory as well as on that of the ordinary chromosomes. The figures on plate LXXI will demonstrate, I believe, that the accessory does not conform to the processes of the other chromosomes. Its isolated position in *one* of the two daughter spermatids shown in figures 26 and 27 is just as apparent as it is in *each* of the two daughter spermatocytes shown in figures 3-10. This characteristic may also be seen in figures 20, 21 and 25. Certain cells in the stages represented in figures 14, 17, 22, 23 may suggest that the accessory chromosome might later divide, and it is upon such as these that Foot and Strobell base much of their argument, but later and more decisive stages demonstrate that it does not do so and this positive evidence has much more value than the presumptive. It is my belief from a careful study of the material and the photographs of Foot and Strobell that not one instance which they figure is an indubitable case of a divided accessory in the second spermatocyte. I do not believe that the indentations in outline, or the light places in the middle of the accessory, have any value as an indication of probable division, for such effects must inevitably occur to delicate structures like the chromosomes in smearing. I would submit that if such evidence is to be used, the chromosomes of the upper group in the anaphase of the second spermatocyte represented in figure 37, plate III of Foot and Strobell, are much more certainly divided than are any of the accessories for which they claim divisions in figures 26-46 of the same plate.

PLATE 71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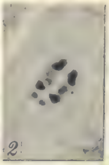
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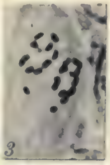
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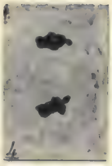
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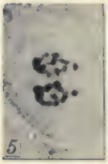
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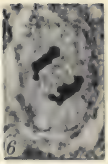
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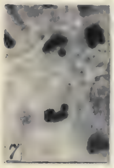
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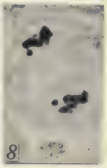
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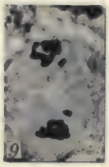
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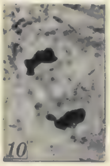
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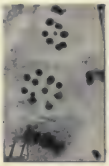
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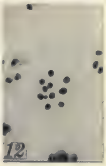
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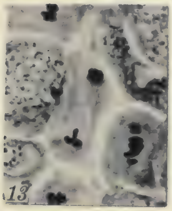
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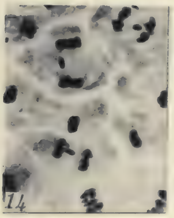
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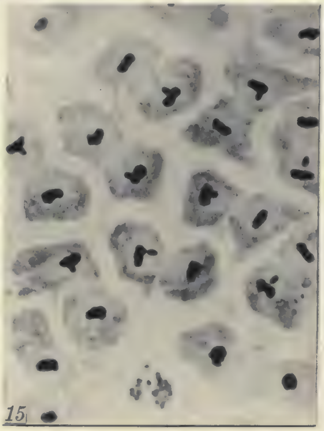
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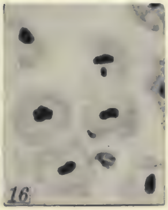
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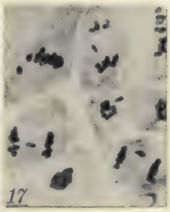
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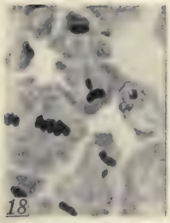
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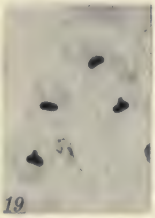
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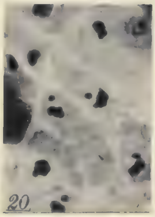
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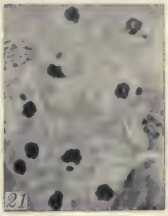
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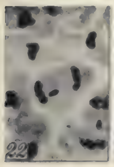
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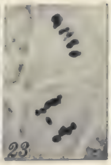
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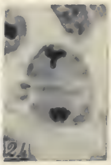
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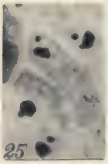
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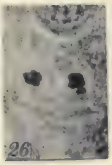
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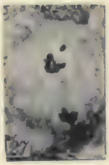
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